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The Movements and Spawning Behaviour of Adult Salmon in the Girnock Burn, A Tributary of the Aberdeenshire Dee, 1986

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The Movements and Spawning Behaviour of Adult Salmon in the Girnock Burn, A Tributary of the Aberdeenshire Dee, 1986

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Introduction

In the past, studies of the spawning migrations and behaviour of Atlantic salmon, *Salmo salar* L., have concentrated on two aspects. Firstly, detailed observations have been made on the spawning behaviour of small numbers of fish, usually in tanks and enclosures (Belding, 1934; Jones, 1959; Beall and Marty, 1983). More recently, descriptions have been given of the gross movements of returning adult fish in coastal waters (Hawkins, Urquhart and Shearer, 1979; Smith, Hawkins and Shearer, 1981; Westerberg, 1982), in estuaries (Stasko, 1975) and within rivers (McCleave, Power and Rommel, 1978; Hawkins and Smith 1986).

Thus, details of the spawning behaviour of individual fish of both sexes have been described for fish in tanks and enclosures, while in tracking studies emphasis has been placed on the overall patterns of movement of different fish, their penetration into the river system, residence times at particular locations, swimming speeds and subsequent progression back down the river. The movements and interactions between fish during the final spawning period have largely gone unobserved and unreported.

This paper describes the spawning behaviour of wild Atlantic salmon within a tributary of a major salmon river. Individual fish were followed by means of radio tracking and by visual observation from the bank. The period of study began on 20 October and ended on 15 December 1986.

Location and Description of the Site

The Girnock burn is a tributary of the Aberdeenshire Dee, a river which enters the North Sea on the east coast of Scotland (Fig. 1). The burn arises approximately 460 m above sea level, to the north and east of Lochnagar (1,115 m), and flows northwards for 9.5 km to join the main River Dee above Ballater, approximately 80 km up stream of the river mouth at Aberdeen. It drains a catchment dominated by a bed of igneous rock and glacial debris with an extensive peat overlay.

The catchment area is 30.7 km^2, the main stream having a mean gradient of 2.4% and a mean width of 6.6 m. More than 80% of the substratum consists of partly submerged boulders (50–70 cm diameter) and stones (ca 30 cm diameter) embedded in gravel (5–10 cm diameter). Within the burn the sands are coarse and concentrated in the major pools, of which those of 0.75 m or deeper make up less than 2% of the total length of the burn.

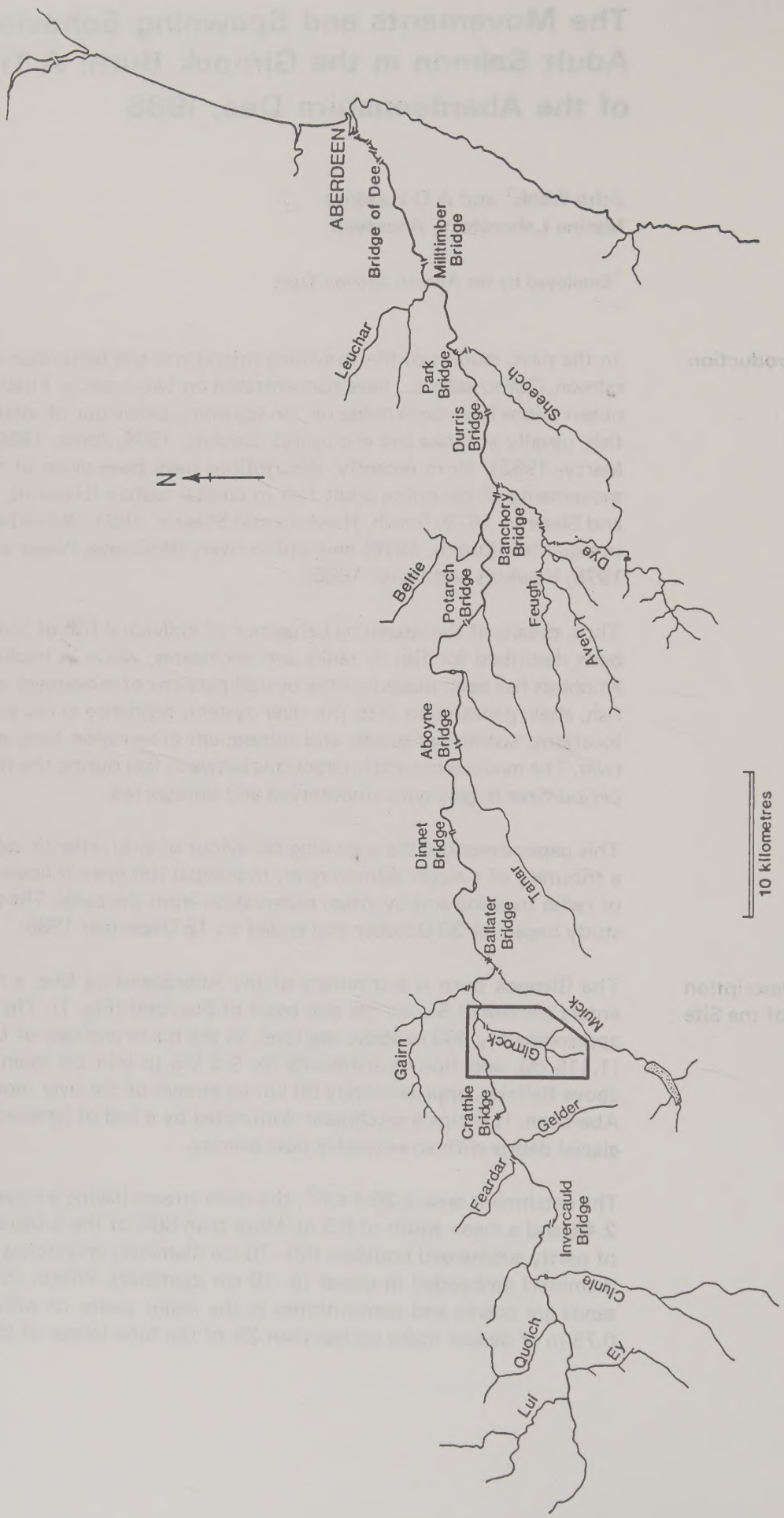

Figure 1 The Aberdeenshire Dee, showing the position of the Girnock Burn in relation to other tributaries.

In the lower reaches, the stream is bordered by a combination of rough pasture and cultivated fields. Higher, the vegetation is predominantly heather, *Erica* sp. and uncultivated grassland. Tree cover extends from the confluence with the main river Dee to approximately 3 km up stream and consists of unmanaged Birch, *Betula* sp., and Alder, *Alnus glutinosa* (L.), with scattered Scots Pine, *Pinus sylvestris* L., and Larch, *Larix* sp. Little, if any, aquatic macroflora are found within the whole length of the burn, although filamentous algae are widespread in the spring and summer (Buck and Hay, 1984).

Historically the burn has been used as a source of water power. There are two remaining weirs, at Littlemill (1.3 km up stream of the confluence with the Dee) and at the Mill of Cosh (1.7 km). Three deer-fence watergates are positioned at 2.2 km, 3.1 km and 3.4 km up stream, two bridges at 3.4 km and 5.5 km, and a vehicle ford at 6.2 km (Fig. 2). A trap to catch ascending adult fish and a descending juvenile trap are positioned close together 0.9 km up stream of the confluence with the Dee, (Buck and Hay, 1984). The Girnock is in a sparsely populated area, with human habitation concentrated around the road bridge carrying the B976 over the burn.

Much of the precipitation in the upper part of the Dee falls as snow over the greater part of winter, the resultant snow melt in the spring giving an 'alpine' pattern of flow. Mean annual rainfall, recorded at the junction of the east burn (Fig. 2) over the period 1966–76 by Buck and Hay (1984), was 700 mm, with a range of 522 mm–836 mm. Mean daily discharge over the same period, measured at the Scottish Development Department (SDD) gauging station was $0.39 m^3 s^{-1}$, with a range of $0.29 m^3 s^{-1}$ to $8.87 m^3 s^{-1}$, and a peak discharge of $22.94 m^3 s^{-1}$.

The water in the burn is characteristically clear and unpolluted, though it is subject to periods of clouding from silt and organic debris (Ross, 1986). Bank erosion is evident at several points, associated with the activities of livestock and vehicles. Peat-derived matter and general leaf and twig debris made up the major proportion of suspended material observed during the period of study.

Conditions During the Study Period

At the start of the study period, up to and including 29 October, the level of water in the burn was low (mean daily discharge $0.147 m^3 s^{-1}$). On 30 October discharge rose to a peak ($1.27 m^3 s^{-1}$), followed by a series of further peaks throughout November (Figs. 3–15).

Water temperature declined over the study period. The main fall took place during the last two weeks of October and continued into November and December (Figs. 3–15). Icing of the surface of the burn took place on 19, 20 and 21 November.

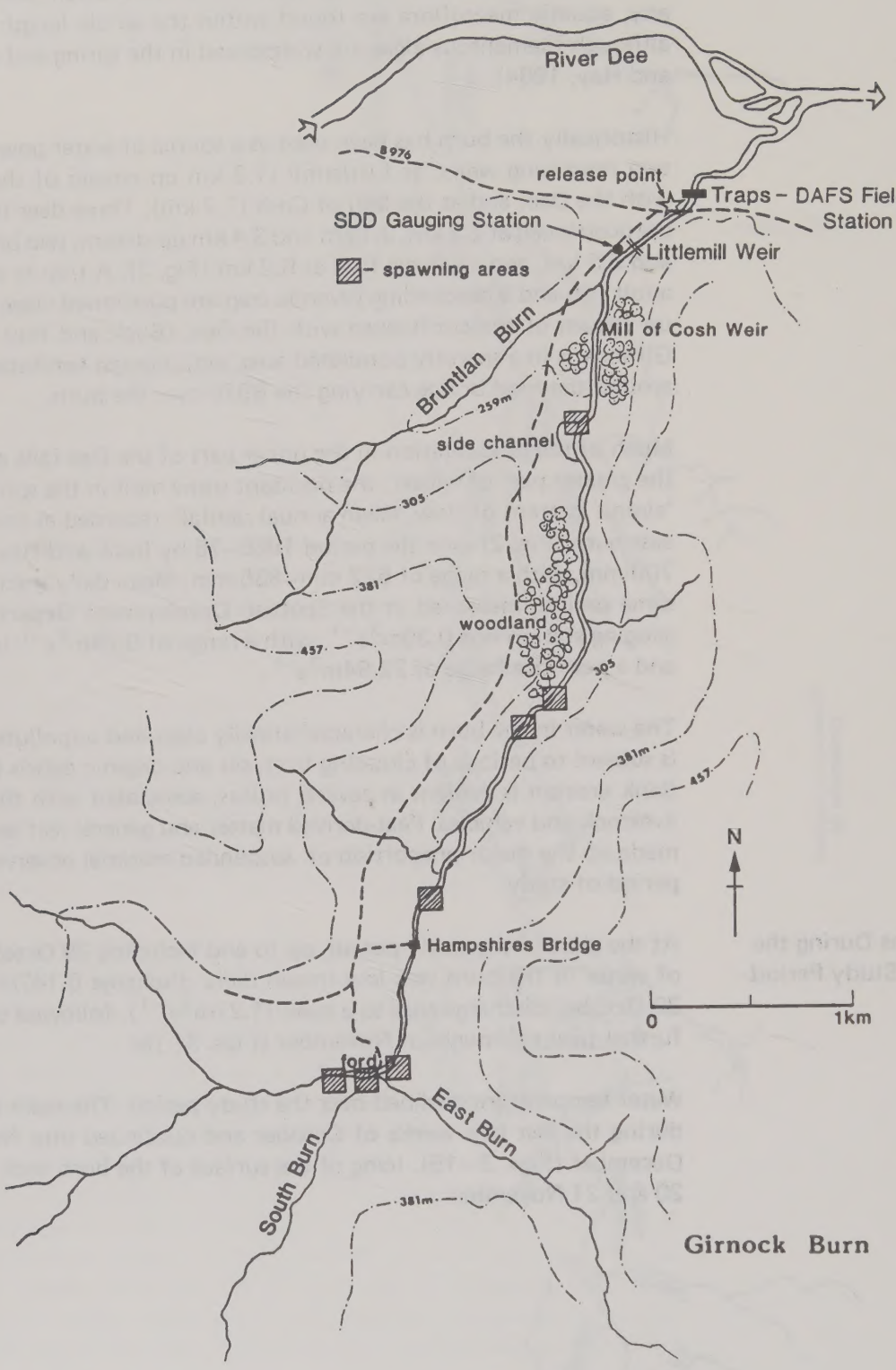

Figure 2. The Girnock Burn. Detail of the relief, and those features referred to in the text.

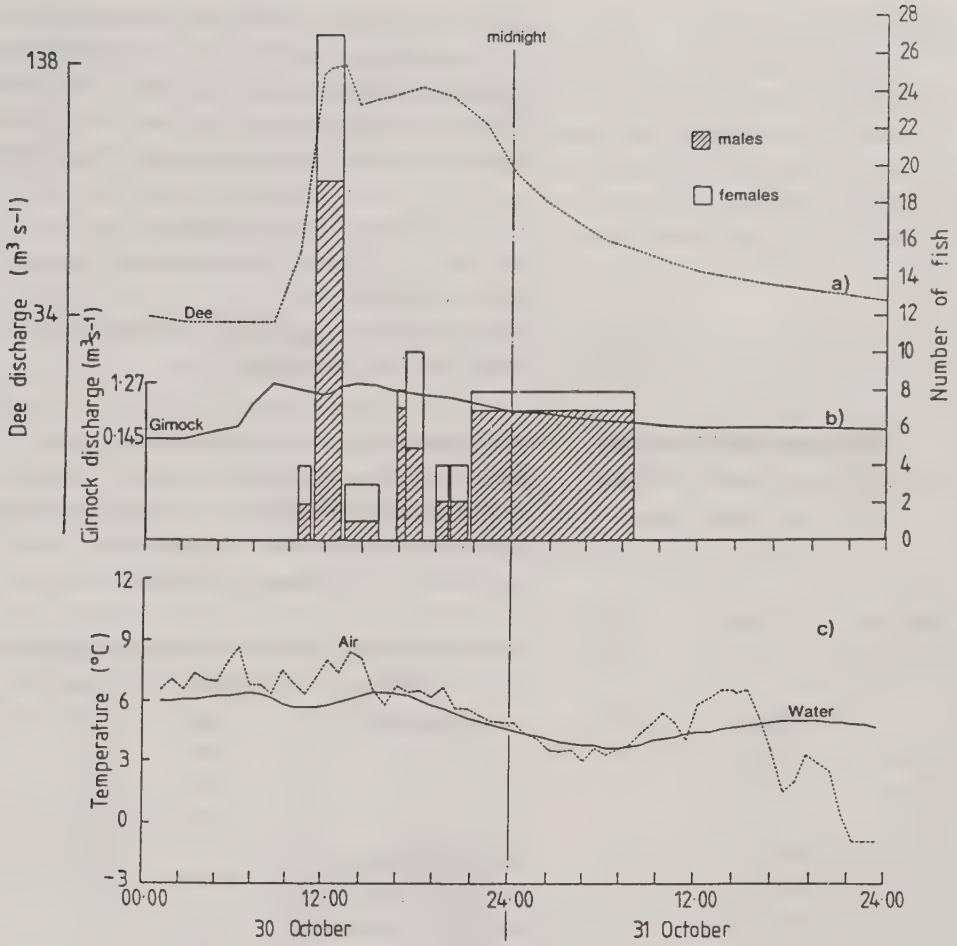

Figure 3. The numbers and sexes of adult salmon intercepted in the ascending trap on 30 and 31 October 1986. The width of each column indicates the time the trap was fishing and the height the numbers of fish caught.
(a) Dee discharge: Polhollick (m^3 s^{-1})
(b) Girnock discharge: Littlemill (m^3 s^{-1})
(c) Air and water temperature (t°C).

The Fish of the Girnock Burn

The burn contains a well studied population of juvenile salmon. Annual smolt production within the burn, measured as spring migrants at the descending trap, has recently ranged from 1,440 (1968) to 3,679 (1977) with a mean of 2,442 (1967–1986). Average salmon parr densities within the burn over the years 1968 to 1979 were 0+, 11.5–79.4 per $100m^2$; 1+, 4.9–30.3 per $100m^2$; 2+, 2.4–16.6 per $100m^2$; 3+, 0.2–1.6 per $100m^2$ (D.W. Hay, personal communication). The majority of smolts leaving the burn (65%) are aged 3 years, with a smaller proportion (31%) of 2 year olds, the remainder being 4 year olds (D.W. Hay, personal communication). A few small trout are encountered, but densities are low. Small eels and lampreys also occur within the burn.

A programme of smolt tagging, using conventional Carlin tags, has shown that a proportion of the Girnock fish return to the Scottish east coast during the period May to July, after only one winter in the sea (ie as grilse) and are caught in coastal nets. Very few Girnock grilse are, however, caught within the river by rod and line, and only a small number of grilse enter the Girnock ascending trap (averaging 12% of the total number of adults returning over the years 1966–1986). The majority of these grilse are males.

Fish tagged as smolts in the burn have been recaptured in the sea off the coast of west Greenland in the autumn, the majority of these having already

spent one winter in the sea. However, by far the greatest number of recaptures are two-sea-winter fish, encountered along the Scottish coast in February, March and April and in the River Dee from February onwards. A few three-sea-winter fish have also been recaptured off the Scottish coast in the spring, and in the river Dee during the spring and summer.

Adult fish may enter the ascending trap on the burn in small numbers in the autumn, but the majority do so in October or November, when their arrival often coincides with early winter spates. The majority of fish entering the ascending trap and the majority of Girnock-tagged fish returning to the burn, are two sea-winter fish.

Materials and Methods

Fish Capture and Tagging

Ascending adult fish entering the burn in 1986 were intercepted by the lower Girnock trap, consisting of a simple deflecting fence and box trap with inscales, constructed of vertical barred screens (13 mm steel rods at 50 mm centres). Over the period of study (20 October–15 December) all ascending fish were intercepted; the numbers are given in Table I.

Table I Numbers of fish entering the ascending trap over the period 30 October–9 November 1986 inclusive. The sea age is given where scale reading was possible

	Male	Female	Total
		30 October	
Grilse (1-sea-winter)	27	5	32
Salmon (2-sea-winter)	27	29	56
Salmon (3-sea-winter)	2	2	4
Others	1	0	1
	57	36	93
		1 November	
Grilse (1-sea-winter)	1	–	1
Salmon (2-sea-winter)	–	2	2
	1	2	3
		9 November	
Grilse (1-sea-winter)	2	8	10
Salmon (2-sea-winter)	11	28	39
Salmon (3-sea-winter)	–	1	1
Others	12	1	13
	25	38	63
TOTAL	83	76	159

The radio-tagged fish were selected from those which entered the ascending trap on 30 October and 9 November. Large fish (>80 cm long), fish badly infected with fungus (*Saprolegnia* sp.), and fish that had been held for long periods were rejected for tagging but were released untagged into the burn. All fish were lightly anaesthetised with a solution of Benzocaine (*ca* 30 parts per million), their fork length measured and scale samples taken.

After tagging, fish were immediately placed into the head of the pool above the juvenile trap, remaining in a dip net until they were able to maintain position in the current. Tagged and untagged fish were released together at night. Eighteen adult salmon were radio-tagged and subsequently released (Table II). Twelve were released on 2 November (taken from those caught on 30 October) and the remaining six were released on 12 November 1986 (taken from those caught on 9 November). As soon as the tagged fish were released, radio-tracking was begun.

Untagged fish were released on three occasions (Table III), 2 November (27), 12 November (21) and 14 November (7). The remainder of the adult fish captured at the trap were stripped and their progeny were placed in the burn as eyed ova the following spring.

Table II Summary of capture and release data for the 18 salmon tagged with radio-transmitters. All these fish were radio-tagged on the day of release

Fish	Sex	Fork length (mm)	Age	Transmitter frequency (mHz)	Date of capture	Date of release	No. days tracked
A	F	66.5	2+.2	104.7040	30.10.86	2.11.86	15
B	M	80.0	3.2	104.7052	"	2.11.86	28
C	M	77.0	2.2	104.7130	"	2.11.86	38
D	F	64.5	3+.2	104.7163	"	2.11.86	15
E	M	72.0	2.2	104.7203	"	2.11.86	28
F	F	69.5	2.2	104.7248	"	2.11.86	13
G	F	69.0	3.2	104.7318	"	2.11.86	14
H	F	67.5	3+.2	104.7353	"	2.11.86	11
I	F	73.0	3.2	104.7399	"	2.11.86	14
J	F	68.0	2.2	104.7455	"	2.11.86	28
K	F	65.0	3.2	104.7025	"	2.11.86	14
L	M	72.5	2+.2	104.7180	"	2.11.86	28
M	M	86.0	2.2	104.7125	9.11.86	12.11.86	16
N	F	72.0	3.2	104.7030	"	12.11.86	12
O	F	69.0	2.2	104.7034	"	12.11.86	5
P	M	80.0	3.2	104.7175	"	12.11.86	18
Q	F	70.0	2+.2	104.7028	"	12.11.86	11
R	F	73.5	2.2	104.7029	"	12.11.86	21

Table III Summary data on the release of radio-tagged and untagged fish. The total number of fish released is given, with the numbers of radio-tagged fish in each group shown in brackets. Twenty five percent of the fish allowed into the burn to spawn were radio-tagged

	Number of fish released			
	Male	Female	Total	Date of Release
Batch 1	17(4)	22(8)	39(12)	2.11.86
Batch 2	12(2)	15(4)	27(6)	12.11.86
Batch 3	2	5	7	14.11.86
Total	31(6)	42(12)	73(18)	

Fish Tracking and Observation

Fish were tracked from the stream bank by means of a digitally pre-tuned receiver and hand-held, folding, bi-directional H-Adcock antenna (Solomon and Storeton-West, 1983). Detection and subsequent location was by means of the system described by Hawkins and Smith (1986), adapted for the precise location of fish at close range by a progressive reduction in the size of the aerial with increasing proximity to the fish.

Radio-tracking was used mainly for long range location, or for tracking fish at night and when water levels were high and visual observation was difficult. Individual fish could sometimes be identified from among those in a group, since the immediate end of the co-axial cable connected to the receiver proved to be directional. Polaroid glasses were used to reduce reflections for observations from the bank.

To supplement tracking from the bank, eight automatic receiving stations (Solomon and Storeton-West, 1983) were spaced out along the length of the burn to record the time of passage of individual fish. To reduce the distance over which fish were detected, antenna lengths were short (one half wavelength). The receiving stations were serviced at least once a day during the main tracking period. Occasionally, the stations failed to register the passage of fish moving rapidly down stream.

Fish positions were recorded by reference to points marked 40 m apart on a 1:10,000 Ordnance survey map, giving an accuracy of ± 5 m. Distance from the confluence with the Dee to each point on the Girnock was calculated from a digital map of the burn stored on computer.

Continuous single point recordings of stream discharge and water and air temperatures were made at the SDD water gauging station and the trap site respectively (Fig. 2).

Spawning Observations

The spawning activities of male and female fish, both tagged and untagged, were recorded in a field note book. A portable video camera was used to record particular aspects of fish behaviour and to supplement the field notes. The final act of spawning (with simultaneous gaping of both sexes and subsequent egg burial by the female) was seen on many occasions, and the participants were identified and their activity noted. In addition, other interactions between male and female fish were also noted. Where the identitification of the primary male participant was not possible, for example because of repeated displacement by other males, the observation was classed as attempted courtship and spawning for that male.

Redd excavation positions were observed and their locations subsequently recorded. Only completed redds or those redd pits where females were subsequently seen performing burial actitvities were recorded as spawning positions.

The Movements of the Ascending Fish

Over the initial observation period of 24–29 October; neither salmon nor sea trout (*Salmo trutta* L.) were observed entering or ascending the burn despite a major increase in flow in the main river (Fig. 3). However, water levels within the burn itself remained low until the morning of 30 October.

The first ascending fish entered the trap on 30 October 1986, as shown in Tables I and IV and illustrated in Figure 3. Other fish entered on 1 November and 9 November. The first fish were observed in the vicinity of the adult ascending trap at 10.19 on 30 October. Recording of the actual time of entry to the trap by the individual fish was often precluded by high water

turbidity. A few fish were observed entering the trap immediately on arrival, particularly when most of the burn discharge was emerging from the area of the entrance. However, other fish entered each time the trap fence was cleared and a pulse of water was generated.

Table IV Numbers and sexes of adult salmon entering the ascending trap on 30 October 1986 in relation to the time of trap operation

Trap Open	Trap Closed	Numbers of fish removed after closure		
		Males	Females	Total
*	10.45	2	2	4
11.15	13.15	19	8	27
13.20	15.20	1	2	3
16.30 d	17.15 d	7	1	8
17.31 d	18.10 d	5	5	10
18.40 d	19.40 d	2	2	4
19.50 d	21.12 d	2	2	4
22.00 d	** d	19	14	33
	Total	57	36	93

* the first fish was observed in the vicinity of the trap at 10.19 hours.

** trap left open until 08.30 on 31 October.

d indicates operation during darkness.

Fish entered the trap just before midday on 30 October, and continued to enter throughout the day (Table IV). Water flow had reached a peak earlier in the morning, and high levels were maintained, with minor fluctuations throughout the day. Several fish (both 2-S-W females and male grilse) entered the trap at dusk or during the first few hours of darkness. More entered later in the night, as water levels fell below the second peak (Fig. 3, Table IV). Three fish also entered on the night of 1 November; these were fish that had failed to enter or reach the trap earlier in the day, not new entrants from the main river Dee. Thus the majority of fish entering the burn did so during the period of peak water flow.

The Release of Fish

Eighteen of the tagged adult salmon were radio tagged and subsequently released above the descending juvenile trap between 2 November and 12 November 1986 (Tables II and III). Contact was then maintained with all eighteen. Some variation in both transmission frequency and signal pulse repetition rate was evident, but individual fish could nevertheless be distinguished readily.

All the radio-tagged fish eventually moved upstream from the release point to areas historically associated with spawning activity in the burn. High water turbidity during periods of elevated discharge prevented detailed visual examination of the movements of untagged fish. However, the time of arrival at the spawning areas, the initiation of spawning activity and limited observations on spawning behaviour were recorded for some untagged individuals.

Rates of up-stream progress for the fish, calculated from the recorded positions of radio-tagged individuals, show wide variations (Tables V, VI and VII).

Table V Rates of up-stream progress of the first batch of radio-tagged salmon released on 2 November 1986. Note that not all fish started at the same position. The initial stationary period shown by the fish has not been included in calculating the rate of progress

Fish	Date and time of commencement of movement	Distance travelled (km)	Duration (h. min)	Rate of Progress (km per day)
A	10.11 02.43	0.312	12.33	0.59
B	9.11 09.15	0.906	00.36	35.20
C	10.11 00.40	0.955	01.55	11.90
D	9.11 10.55	1.410	12.10	2.24
F	10.11 23.08	1.919	15.34	2.95
G	9.11 20.07	2.193	18.49	2.79
H (a)	9.11 20.09	1.525	7.32	4.85
(b)	10.11 03.41	0.383	18.59	0.48
I	10.11 15.25	0.881	16.16	1.24
J	10.11 11.10	3.262	7.30	10.43
K	9.11 22.29	0.178	11.34	0.36
L	14.11 09.36	0.311	00.14	31.90

Table VI Rate of up-stream progress associated with extreme low water discharges (0.089–0.135 $m^3 s^{-1}$), 4–8 November 1986

The observations are made in various parts of the burn

Fish	Date and time of commencement of movement	Distance travelled (km)	Duration (h. min)	Rate of Progress (km per day)
A (a)	4.11 18.52	0.035	0.65	0.077
(b)	8.11 15.10	0.040	0.20	5.760
D	8.11 15.30	0.021	0.25	1.230
L	3.11 10.30	0.730	11.75	1.500
*	6.11 13.50	0.190	0.18	15.400

* denotes movements of untagged male, moving to a female initiating cutting activities.

Table VII The rates of progress of the second batch of salmon during their initial phase of up-stream movement, after release on 12 November 1986

Fish	Date and time of commencement of movement	Distance travelled (km)	Duration (h. min)	Rate of Progress (km per day)
N	13.11 08.30	1.40	4.10	10.6
M	13.11 08.30	0.86	6.54	3.1
Q	13.11 12.20	0.17	2.42	1.6
R	13.11 13.04	0.30	1.34	4.6

Movements of Radio-tagged Females

Eight radio-tagged females were released on the night of 2 November 1986 (together with four males) and four more on the night of 12 November.

Figures 4, 5, 6, 7 and 8 illustrate the movements and activities of the tagged females, together with corresponding details of discharge and water temperature over the observation period.

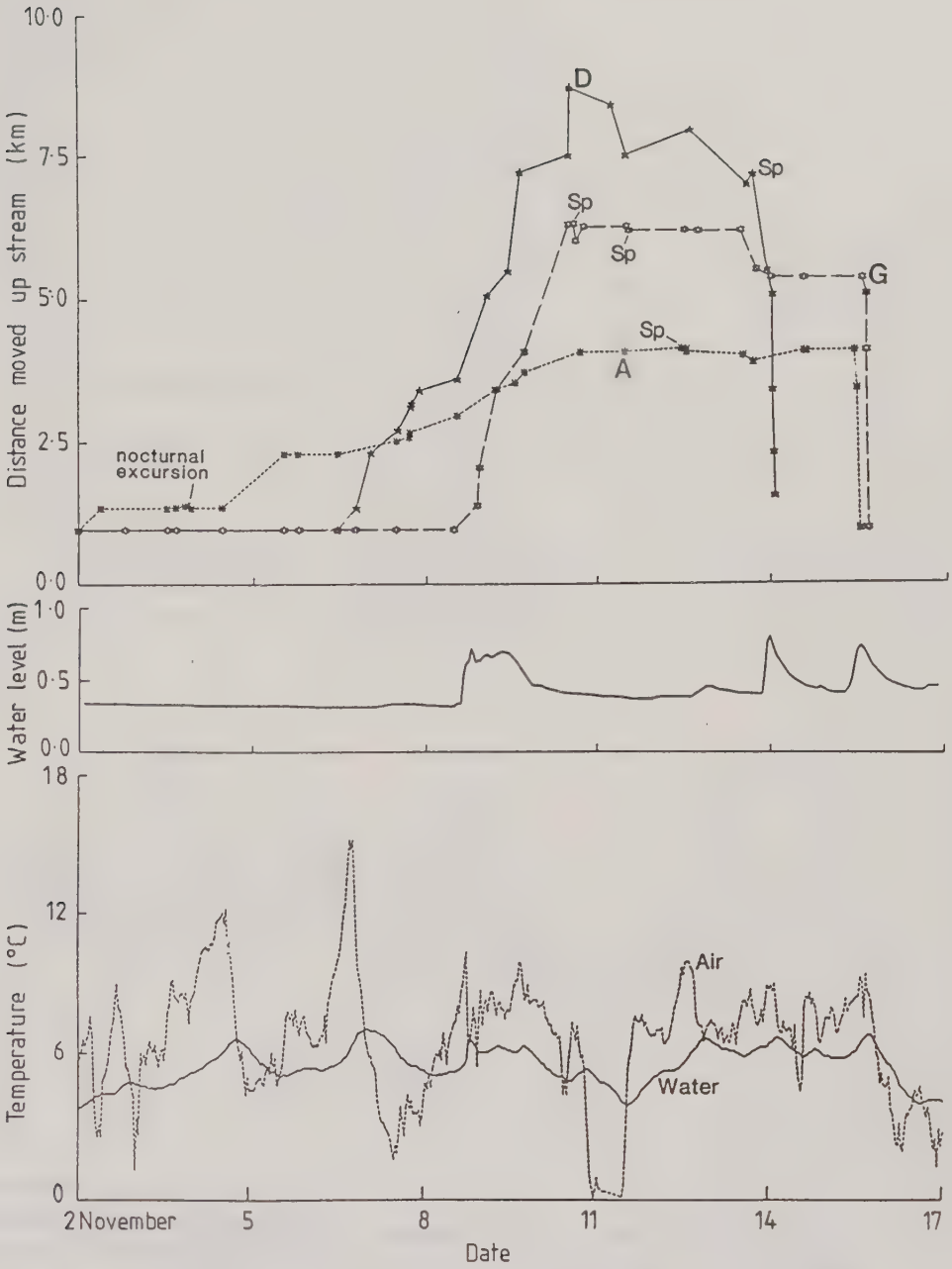

Figure 4. The movements and spawning behaviour of three radio-tagged female Atlantic salmon in the Girnock Burn, released in the first batch of fish, on 2 November 1986. The water level at Littlemill, and air and water temperatures at the trap site are shown.

Fish A, D and G. Sp: Spawning.

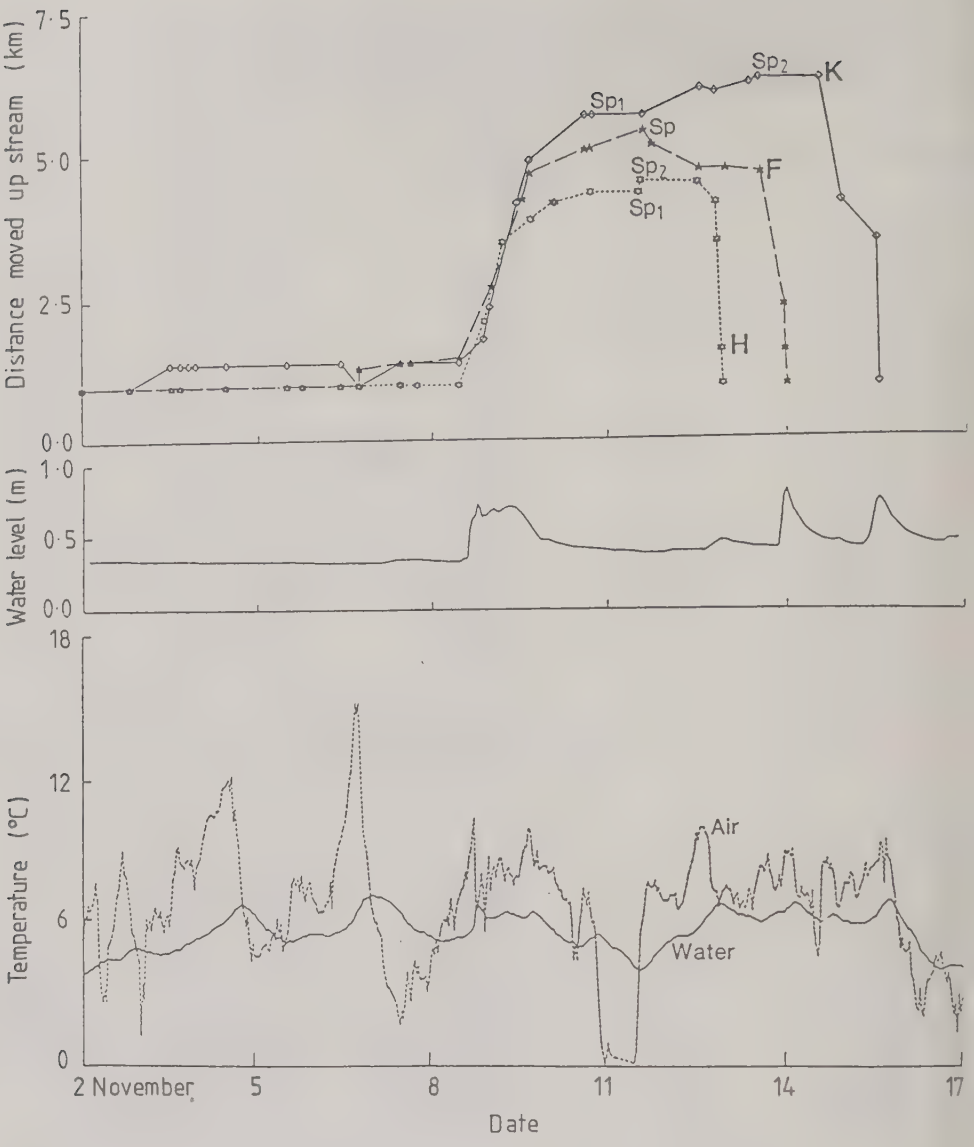

Figure 5. **The movements and spawning behaviour of three radio-tagged female Atlantic salmon in the Girnock Burn, released in the first batch of fish on the 2 November 1986. The water level at the Littlemill gauge and air and water temperatures at the trap site are shown.**

Fish F, H and K. Sp: Spawning.

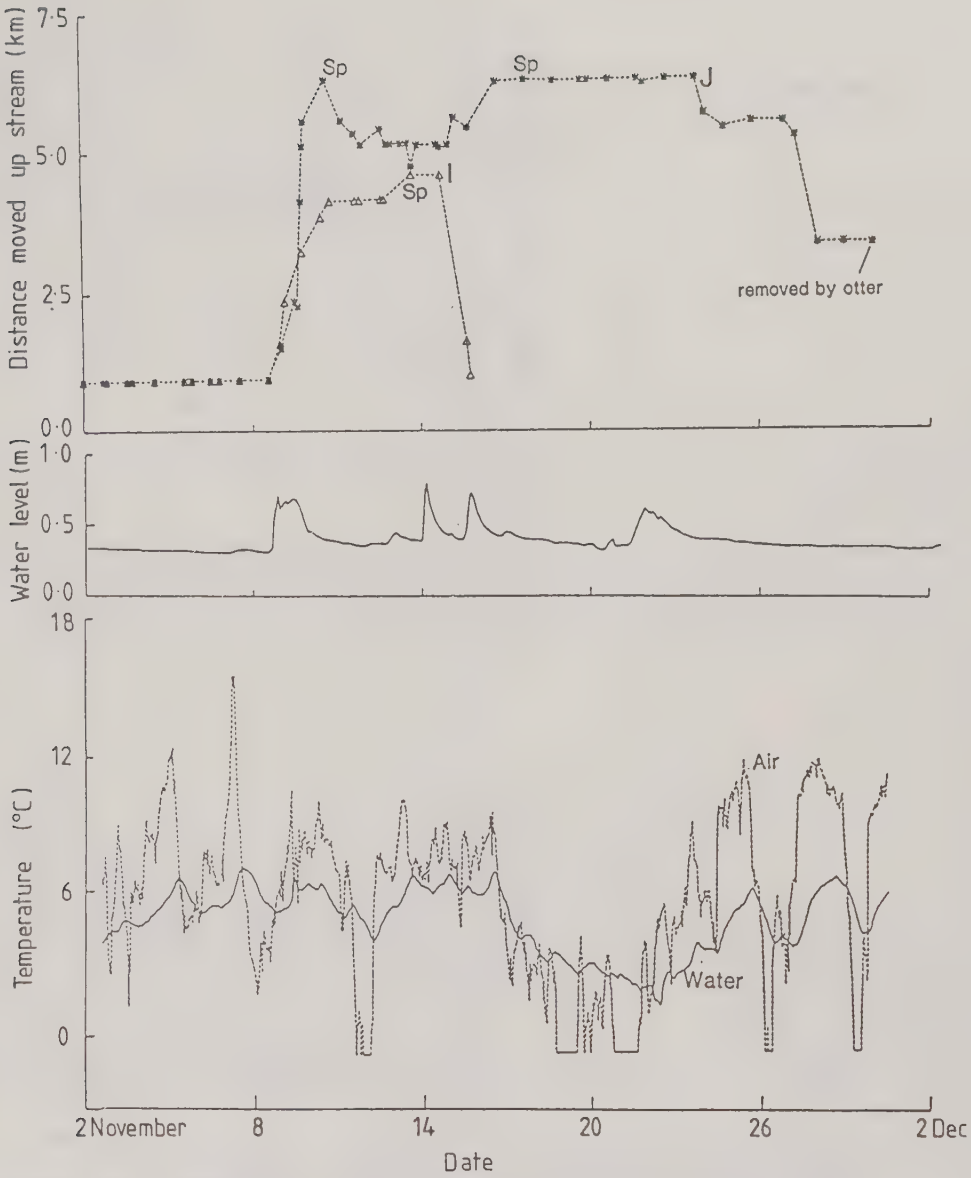

Figure 6. The movements and spawning behaviour of the remaining two radio-tagged female Atlantic salmon in the Girnock Burn, released in the first batch of fish on 2 November 1986. The water level at Littlemill and air and water temperatures at the trap site are shown.

Fish I and J. Sp: Spawning

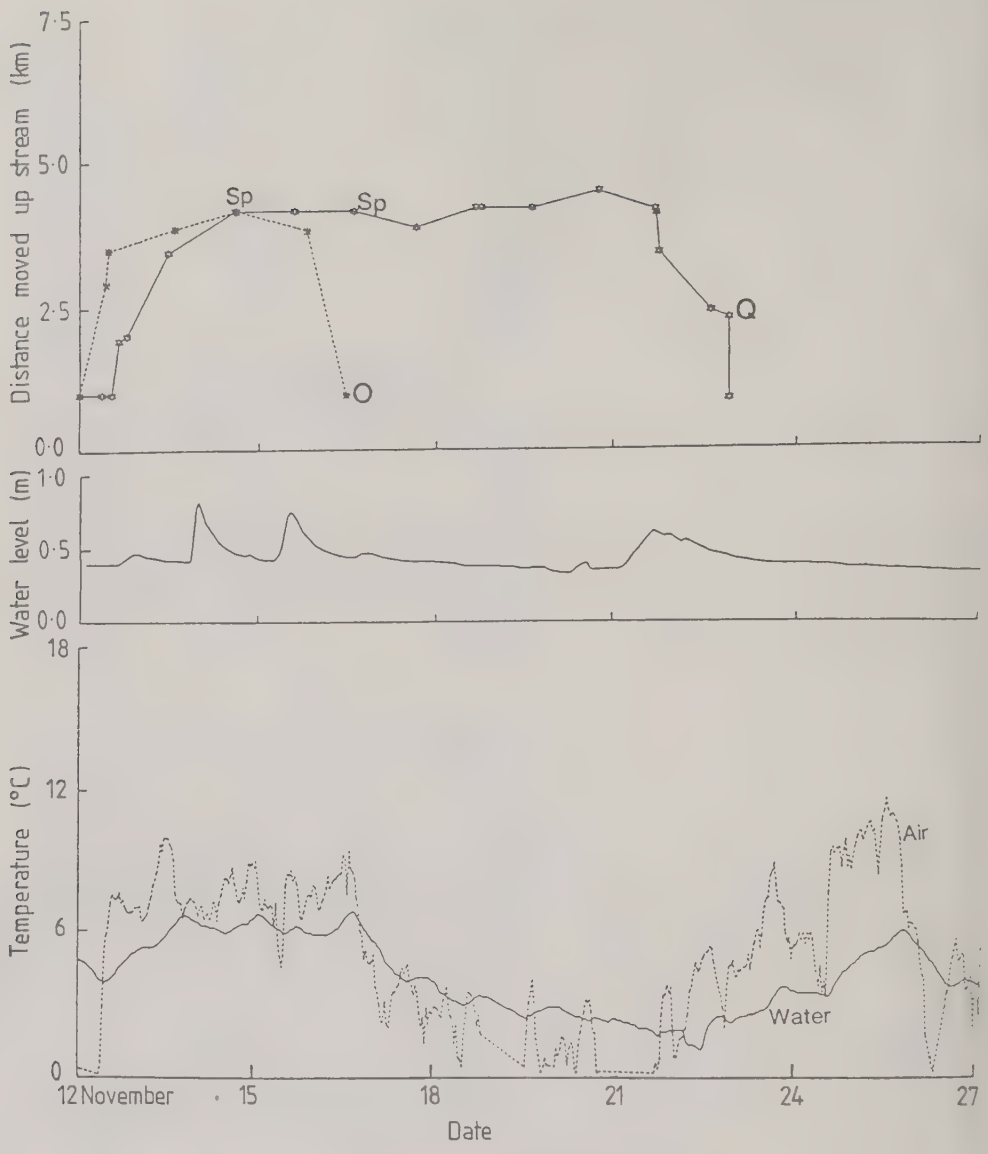

Figure 7. **The movements and spawning behaviour of two radio-tagged female Atlantic salmon in the Girnock burn, released in the second batch of fish, on 12 November 1986. The water levels at the Littlemill gauge and air and water temperatures at the trap site are shown.**

Fish O and Q. Sp: Spawning.

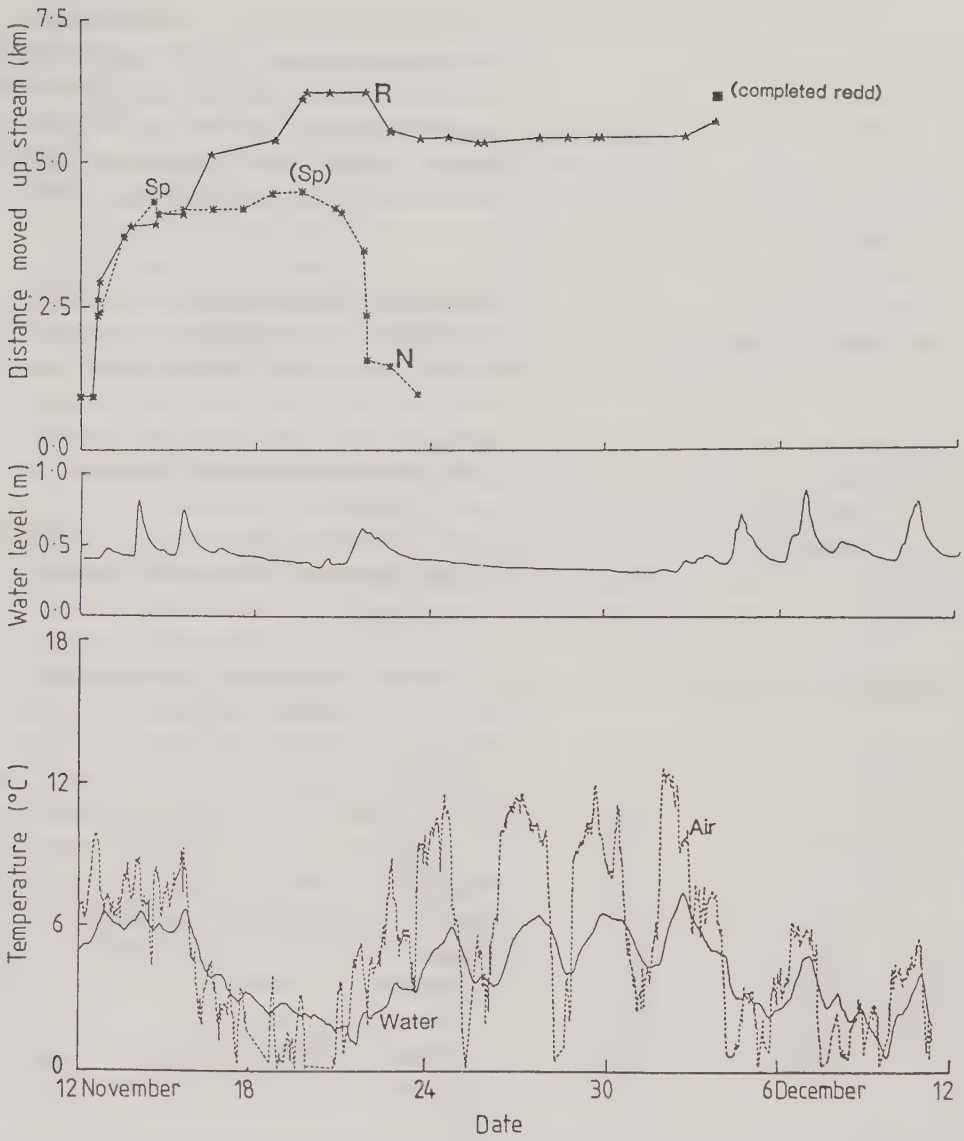

Figure 8. The movements and spawning behaviour of two radio-tagged female Atlantic salmon in the Girnock burn, released in the second batch of fish on 12 November 1986. The water levels at the Littlemill gauge and air and water temperatures at the trap site are shown.

Fish R and N. Sp: Spawning. (Sp): Fish observed in vicinity of complete redd.

Immediately after release, the first batch of females remained in the lower part of the burn. Short return excursions up stream (tens of metres) from the lower pools were occasionally made by these fish, one is shown for tagged fish A in Figure 4 but they are not recorded in Figures 5 and 6. Several untagged females were seen moving during periods of darkness, the fish making short excursions, sometimes lasting several hours, from the main pools.

Tagged fish A and then D were the first of this batch to move significant distances up stream from the release point. Fish A moved slowly but progressively up stream and eventually spawned on 12 November quite low down the burn (Fig. 4). D showed an initial delay but then moved quite quickly to the uppermost part of the burn later returning downstream a short distance to spawn on 14 November (Fig. 4).

Both fish struggled over stones and through shallow channels to make progress up stream under conditions of low flow.

Unlike fish A and D the majority of the first batch of tagged females did not move up stream until 9 November. Then with many untagged females they moved up stream together, as shown for fish G, F, H, K, I and J in Figures 4, 5 and 6. The concerted movement of these fish took place during an increase in water level within the burn and in most instances it eventually resulted in these females moving to their final spawning positions. With the exception of female D, there was no evidence of the females ascending to levels in the burn above the points at which they eventually spawned. Nor was there evidence of any relationship within each batch between the timing of ascent from the release site and subsequent spawning time and position.

The spawning positions of the first group of tagged females are indicated in Figures 4, 5 and 6. Females G, K, H and J each spawned on two occasions.

With the exception of female J, descent from the burn was initiated within 1–4 days of the final observed instance of spawning activity. Of those fish returning to the area of the trap, females A and G descended in daylight during periods of elevated discharge, whereas females D, F, K and I also descended when burn discharge was elevated, but during darkness. Fish H descended during darkness when discharge was only slightly elevated above basal levels. Female J stayed longer in the burn that the other females from the first batch, with movements both up and down stream being observed after the first recorded spawning on 11 November and continuing until the second spawning on the 18th (Fig. 6). Subsequently this fish remained at the spawning site, returning down stream slowly at the end of November, eventually being removed from the burn by an otter.

The second batch of females was released on 12 November; their movements are shown in Figures 7 and 8. Unlike the first batch of females, most of which waited for an elevation in burn discharge, all these fish moved directly up stream, water levels already being elevated above basal levels. With the exception of female R, the second batch of females did not penetrate as far up stream as the first batch and their spawning positions were not as widely distributed. Observation from the bank showed that this compression of the range of movement and spawning activity also occurred in untagged females released at the same time. Over all, however, the behaviour of this second batch of females was very similar to that of the first batch, in that the fish moved up stream, initially under condition of

elevated flow, and then spawned. A notable exception was the lack of repeat spawning in the second batch.

Female R, which penetrated further up stream than the others of its batch (Fig. 8), was not seen to spawn, although two unfinished redds were observed on the morning of 23 November at the head of a pool in which this fish had remained for some time. A tagged male (fish L) was in the same pool for several days over the same period. Female R was eventually found incapacitated and fully spent, some 0.49 km up stream of its former position, on the morning of 4 December during a period of mild weather; a new redd was observed below the entry of the East burn, some 280 m further up stream.

The descent of the second group of tagged females is shown in Figures 7 and 8. In the later stages of their down-stream movements, females Q and O descended during the hours of darkness and over periods of elevated discharge. Female N descended in daylight during the spate on 22 November. Rates of down-stream progress are given in Table VIII.

Table VIII. The rate of progress of radio-tagged female salmon kelts down stream from the spawning areas.

Fish	Date and time of commencement of movement	Distance travelled downstream (km)	Duration (h. min)	Rate of progress (km per day)
A	16.11 08.10	3.119	2.40	28.1
D	14.11 20.40	4.536	3.36	31.2
F	14.11 10.44	3.012	10.11	7.2
G	16.11 12.40	4.108	1.10	79.0
K	15.12 19.12	3.444	10.00	8.3
N	22.11 12.32	1.907	2.33	17.9
Q	23.11 17.35	1.485	7.36	4.6

Movements of Radio-tagged Males

Four radio-tagged males were released in the first batch of fish on the night of 2 November and two more were released on the night of 12 November. Details of the fish are given in Table II.

Figures 9, 10, 11 and 12 show the movements of the males released in the first batch (L, B, E and C) and Figure 13 the movements of the males in the second batch (M and P). Gross movements within the catchment are shown, together with the distribution and frequency of observed spawning activities, up to the period of active descent from the higher levels of the catchment to the area of the release point, or death and subsequent removal.

The movements of the male fish tended to be synchronised with those of the females. Compare, for example, the movements of the male fish in Figures 10 and 12 with those of the females in Figures 4, 5 and 6. Males were commonly observed following females, as shown in Figure 14.

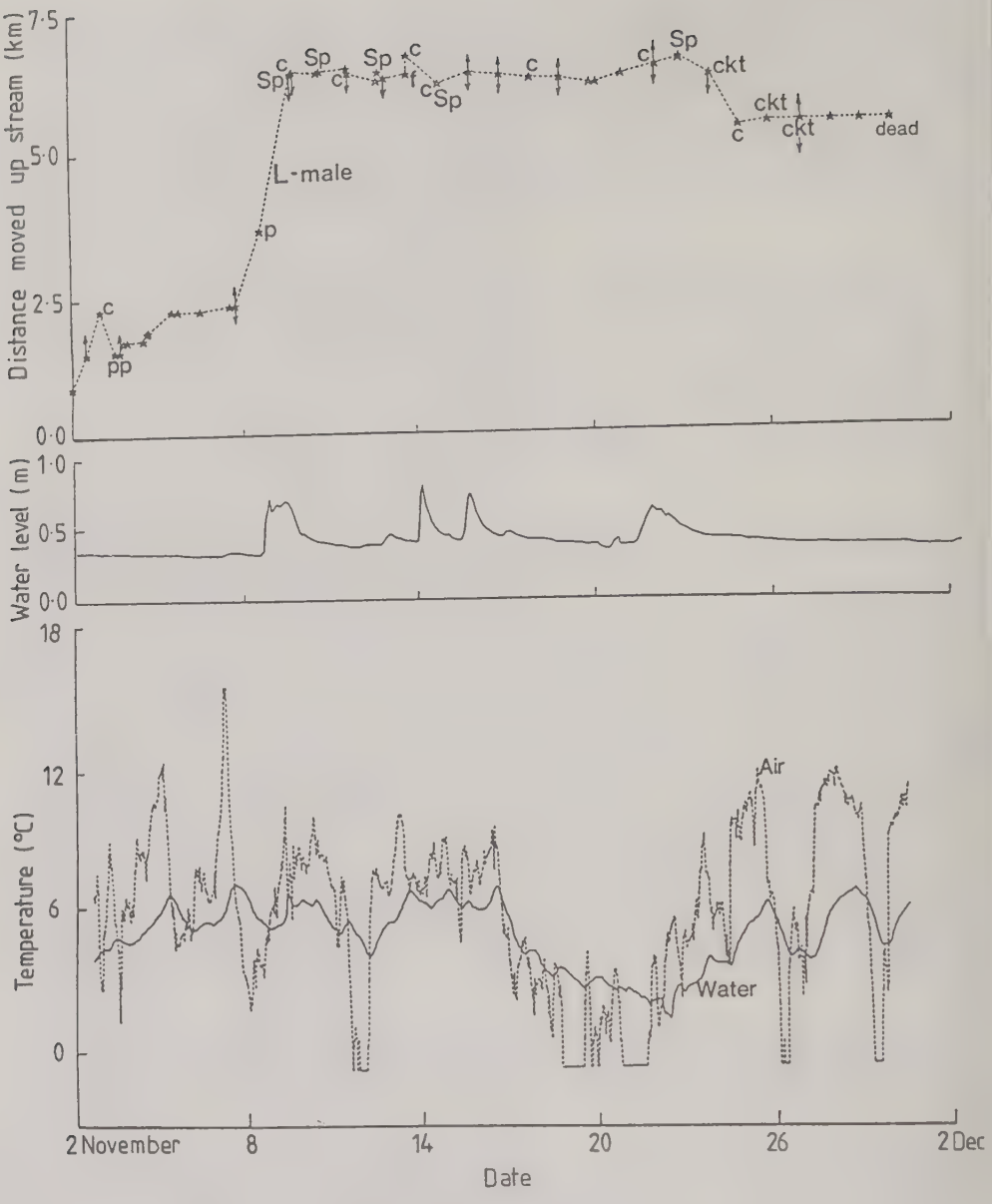

Figure 9. **The movements and activities of a single radio-tagged male Atlantic salmon in the Girnock burn, released in the first batch of fish on 2 November 1986. The water levels at the Littlemill gauge and air and water temperatures at the trap site are shown.**

Fish L. c: Courting maiden female. f: Fighting other male. p: Paired maiden female. Sp: Spawning. ckt: Courting kelt.

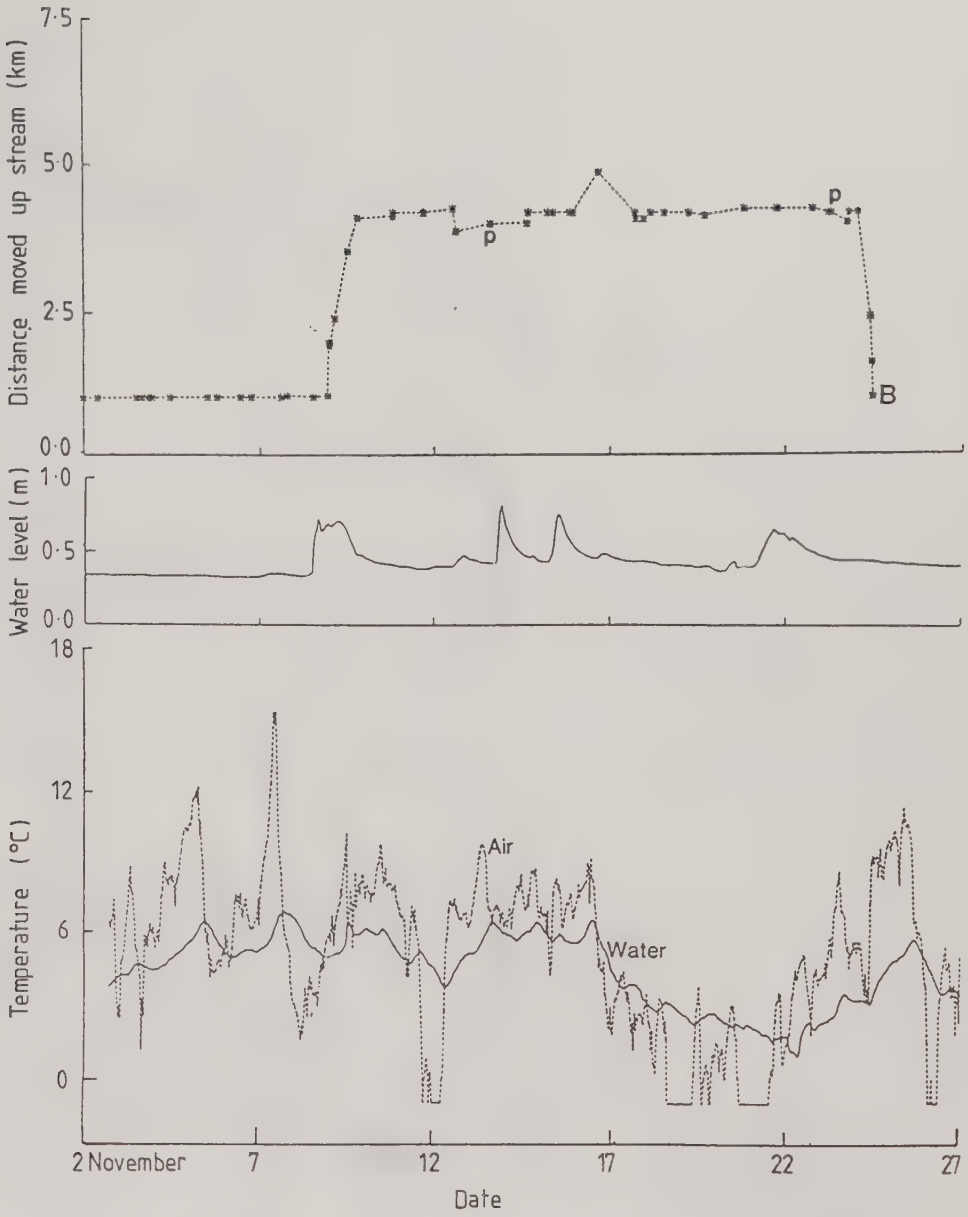

Figure 10. The movements and activities of a single radio-tagged male Atlantic salmon in the Girnock burn, released in the first batch of fish on 2 November 1986. The water level at the Littlemill gauge and air and water temperatures at the trap site are shown.

Fish B. Sp: Spawning. p: Paired maiden female.

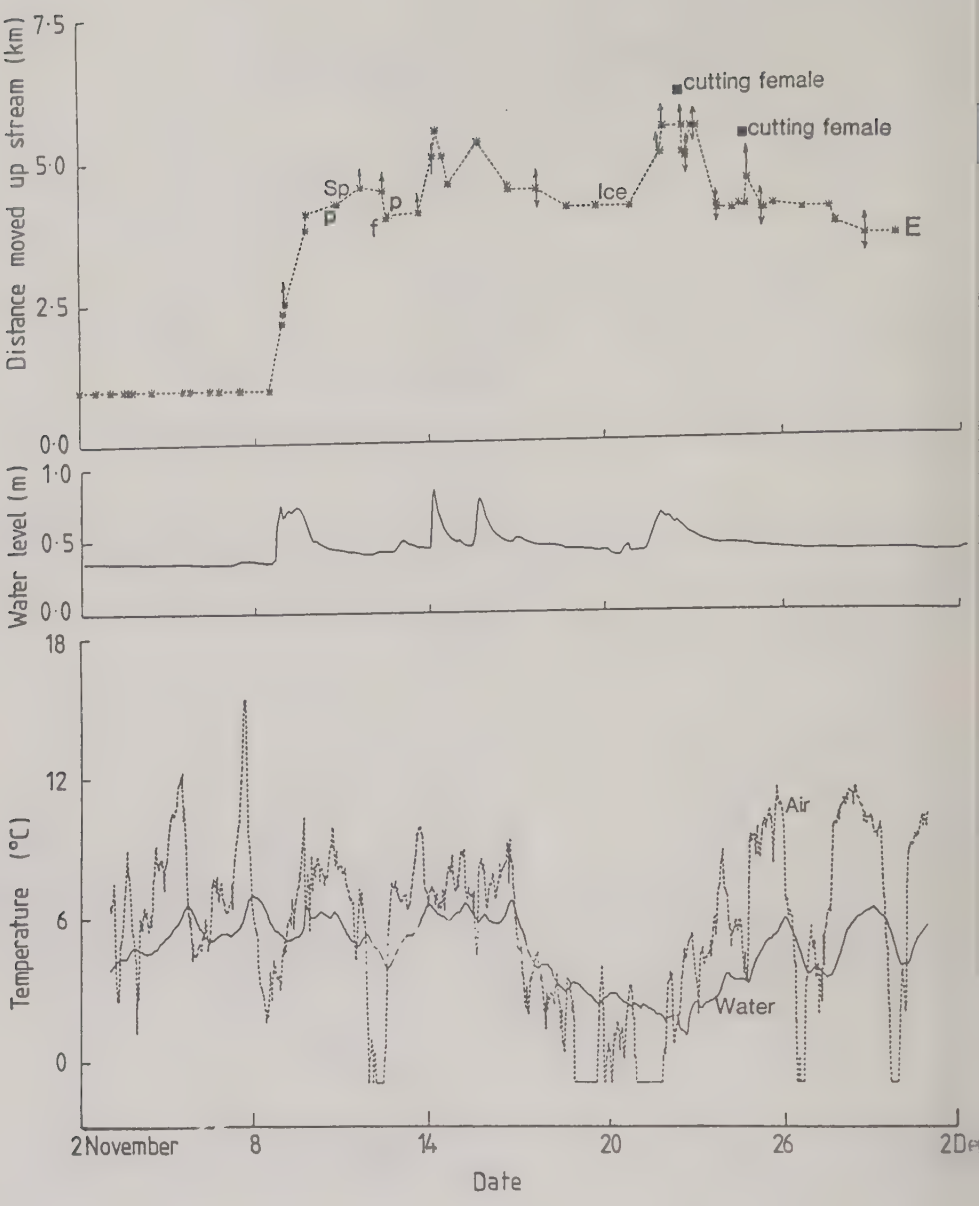

Figure 11. The movements and activities of a single radio-tagged male Atlantic salmon in the Girnock burn, released in the first batch of fish on 2 November 1986. The water levels at the Littlemill gauge and air and water temperatures at the trap site are shown.

Fish E. p: Paired maiden female. f: Fighting other male. Sp: Spawning

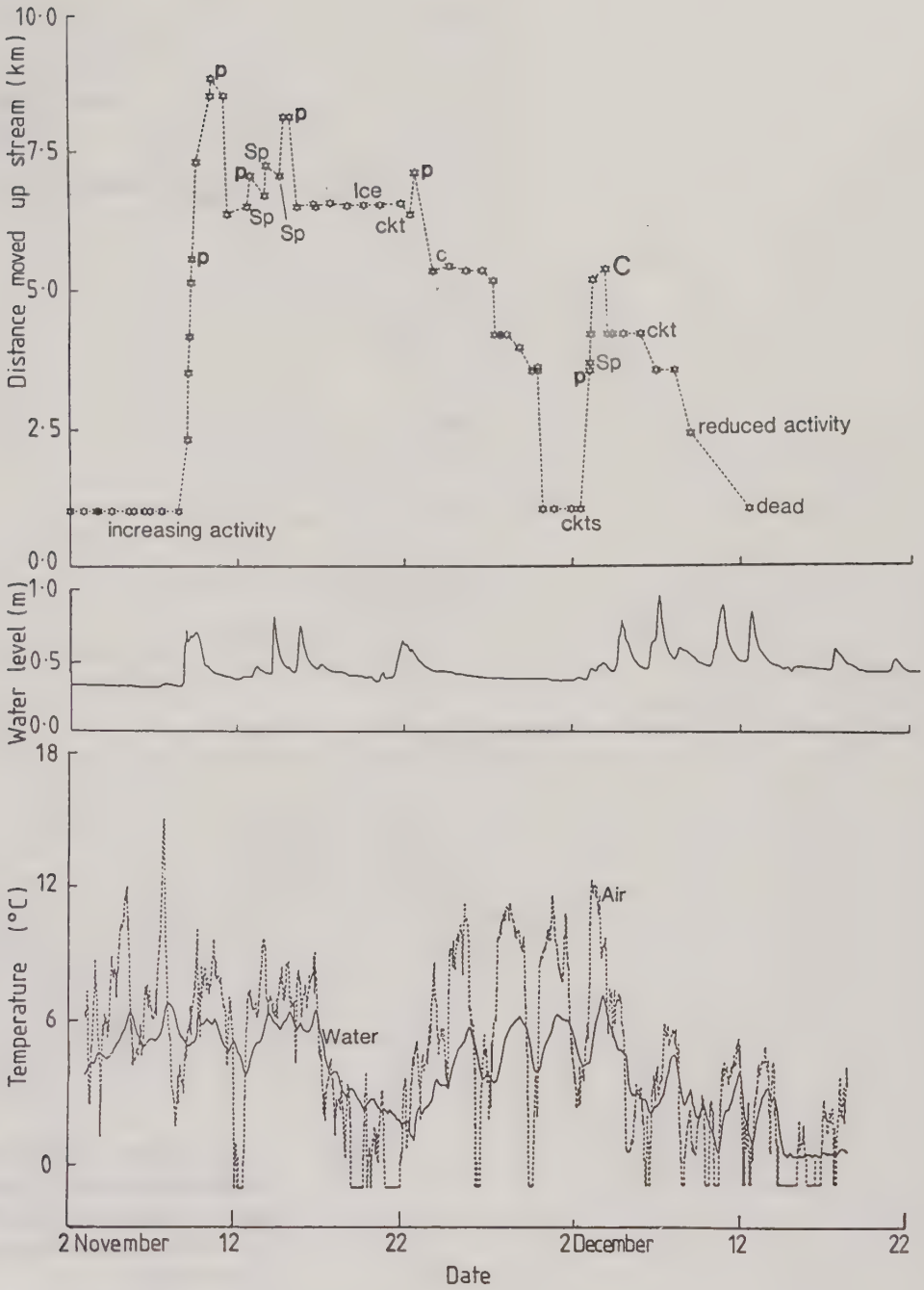

Figure 12. The movements and activities of a single radio-tagged male Atlantic salmon in the Girnock burn, released in the first batch of fish on 2 November 1986. The water levels at the Littlemill gauge and air and water temperatures at the trap site are shown.

Fish C. p: Paired maiden female. Sp: Spawning. c: Courting maiden female. ckt: Courting kelt

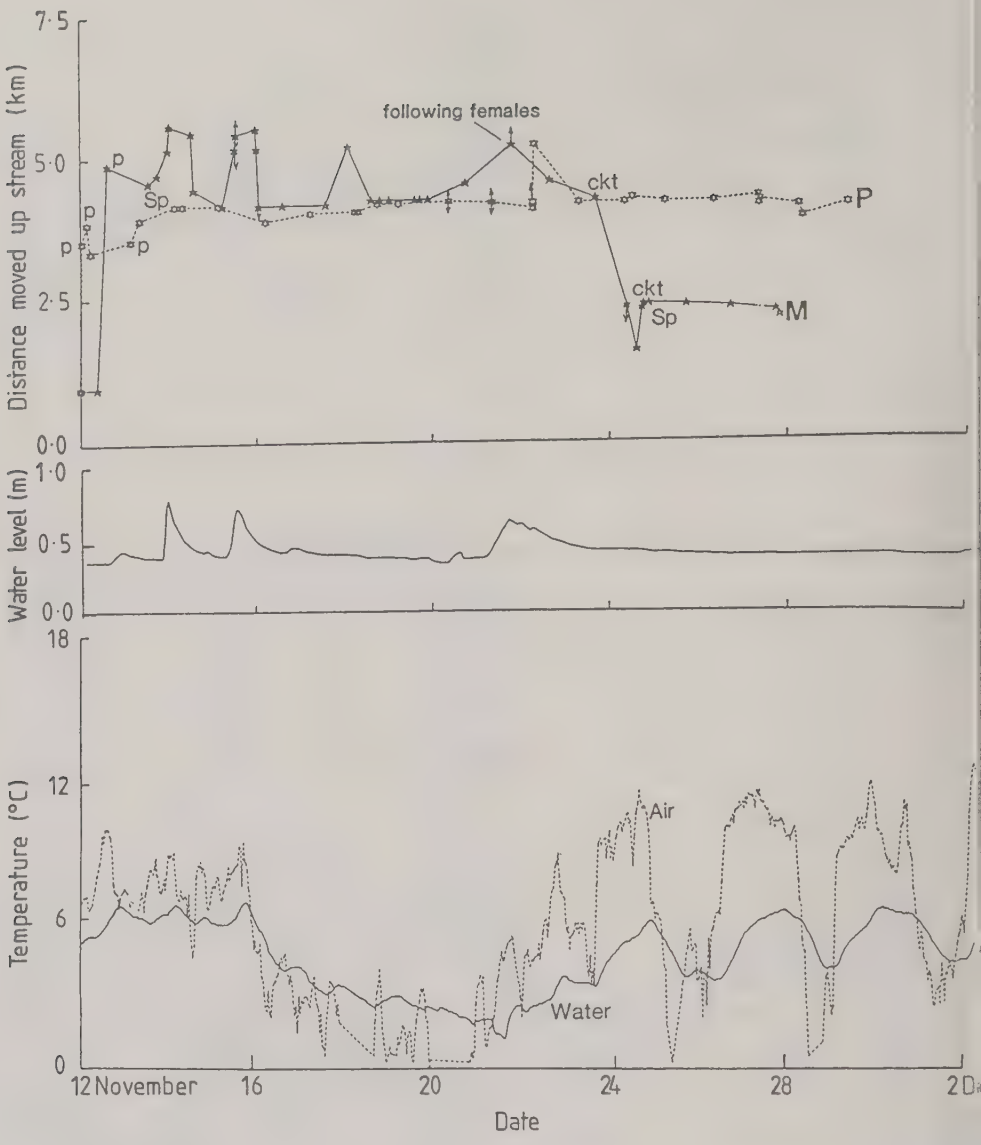

Figure 13. The movements and activities of two radio-tagged male Atlantic salmon in the Girnock burn released in the second batch of fish on 12 November. The water levels at the Littlemill gauge and air and water temperatures at the trap site are shown.

Fish P and M. p: Paired maiden female. Sp: Spawning. ckt: Courting kelt

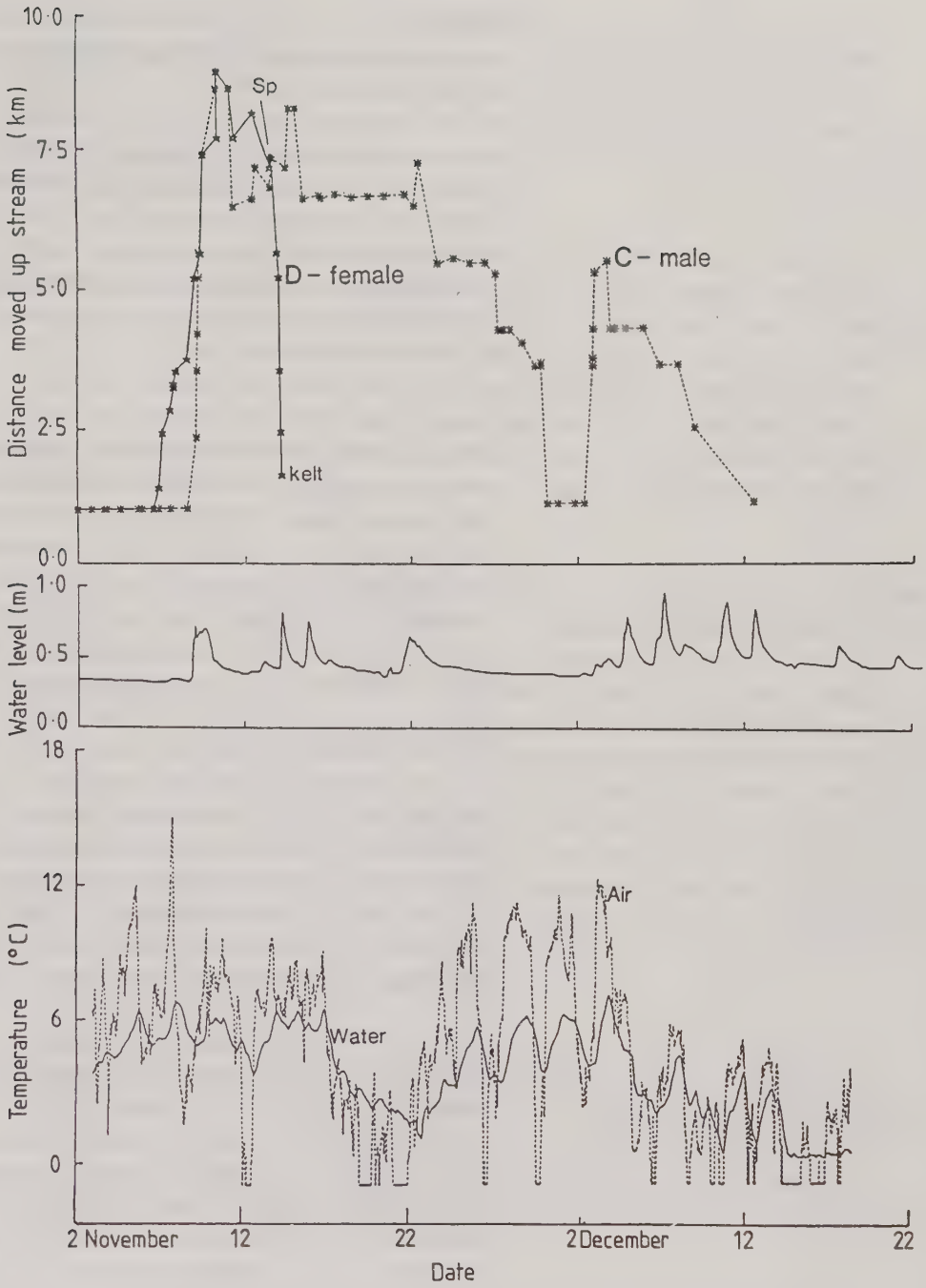

Figure 14. The movements and activities of a single radio-tagged male and a single female in the Girnock burn both released in the first batch of fish on 2 November 1986. The water levels at the Littlemill gauge and air and water temperatures at the trap site are shown.

Fish C, male and Fish D, female. Sp: Spawning.

Male fish did not move or remain up stream of the highest maiden females within the catchment until spawning activities declined in the later stages of the study period.

Short range excursions of less than 1–8 m are not illustrated in all the figures, but it should be noted that such excursions were common for both tagged and untagged male members of the spawning population, particularly after the start of spawning activities within the catchment (5–9 November). The movements were typically continuous, the fish showing repeated excursions both up and down stream, together with traversing of the stream channel.

Despite low discharge levels at the time of release on 2 November, Male L (Fig. 9) moved immediately up stream, reaching a point 1.3 km from the release point on 3 November, only to descend 0.7 km back down stream by the following day (4 November). These early movements were associated with the ascent of a small group of untagged females, which by 6 November had reached a level some 4.1 km upstream. Over the next 14 days fish L remained very active, ascending to the level of the confluence with the south burn, and remaining in the higher and middle reaches of the main stem of the burn until it was removed dead on 30 November.

Males B and E remained in the area of the release point until the spate of the 9th November. During the period 3–9 November, an increase in activity was evident, the fish, especially the males, remaining at the release point, with frequent jumping, excursions to the head of the pool and repeated approaches to those females remaining (the latter typically lying on the pool bottom). The remainder of this first batch of both tagged and untagged fish, males and females, eventually proceeded further up stream on 9 and 10 November as water flow increased.

Males B and E (Figs. 10 and 11) subsequently moved up and down stream within the lowest major spawning area over the greater part of the spawning period. Both males were active within a comparatively short length of the burn, with frequent excursions up and down stream, the fish following the movements of maiden females and descending kelts. Both fish were observed to spawn successfully on one occasion only. Male B subsequently descended the burn on 24 November during the hours of darkness. Male E was recovered in an incapacitated state on 30 November.

Male C (Figs. 12 and 14), from the first batch, also remained close to the release point until the spate on 9 November. It then ascended the burn in close association with tagged female D (Figs. 4 and 14), eventually penetrating higher up the burn than any other adult male over the observation period. It remained within the upper reaches of the main stem of the burn and was subsequently observed to spawn successfully on three occasions with other females at sites below the level of its initial penetration. From 23 November the fish descended the burn over a period of seven days to reach the release area. However, on 4 and 5 of December the fish ascended the burn once more, reaching the level of the Hampshires bridge. It spawned once again during this period and was later found dead at the release point on 12 December.

Of the second batch of fish, released on 12 November, male M remained at the release point for a few more hours but moved up stream from the release point at mid-day on 13 November (Fig. 13). Like male L, released earlier, male M eventually remained within the lower spawning area. Periods of intense activity took place on 17, 23 and 28 November, with repeated short range excursions (*ca* 10–50 m) up and downstream, and across the

stream channel. On 23 November, male M was observed with male B following spent females down stream and reaching the area of the confluence with the Bruntlan Burn (Fig. 2). Later, fish M moved back up stream to spawn with a female grilse in a side channel some 1.3 km above the release point. It was last observed, stranded, just below its final spawning position, on the afternoon of 30 November.

Male P moved from the release point very quickly after release, ascending to a female grilse cutting a redd 3.9 km up stream. This male showed little movement away from the lowest major spawning area, spending comparatively long periods of time in the larger pools, particularly during cold periods with low discharge. A major excursion took place later, coinciding with a similar movement by a number of untagged males, and included some spawning activity 4.1 km upstream. Males M and P both showed evidence of rapid physical deterioration, with extensive superficial damage and associated fungal infections.

he Swimming Characteristics of the Fish

When flood conditions did not prevail, fish moved through those parts of the burn channel with the greatest flow. During periods of high discharge, the movements of fish were more erratic. They tended to avoid the areas of greatest flow (> 1 m s^{-1}) or traversed them by burst swimming. Indeed, they tended to move to and from positions close to the bank or from positions close to obstructions within the channel, like rocks or root masses. Their net up stream progress was the cumulative result of episodic bursts of movement rather than continuous swimming. In areas with few large stones and uniform channel topography (with comparatively simple flow regimes) the movements of the fish were more continuous, with few rest periods. In the larger, deeper pools, however, the movement of fish slowed, particularly where pools were up stream of areas of comparatively broken flow and steep gradient (for example a pool at 3.4 km).

Having entered a major pool (from down stream), fish of both sexes characteristically showed a short period of inactivity in the tail of the pool and then made their way slowly up stream, either continuing on out of the pool, or remaining in an area of slack water (typically in the main body of the pool). Sometimes they moved close to the bank or to a position down stream of an obstruction, typically a large stone or a section of collapsed bank.

Some holding areas for fish were located below potential obstructions. These were either very large stones or fallen trees which channelled the water flow. There was some delay in the movement of fish past these obstacles, though often only for a matter of minutes.

Examples of the rates of up stream progress of fish under differing conditions are given in Tables V, VI and VII. Rates of downstream movement of female kelts are provided in Table VIII.

Differences in Movements Between Males and Females

Some of the fish, both tagged and untagged, males and females, moved up stream even during periods of comparatively low discharge, as illustrated by Figures 4 and 8. Such movements took place both by day and by night, particularly in the first batch of fish to be released. Other fish, however, remained in the pool where they were released, and subsequently only moved up stream when discharge rose above basal levels (for example, females G, H, I and J). Some females moved only under cover of darkness, lying up during daylight hours in deeper pools or under larger stones and bank (for example, fish A, 18.52–19.57 on 4 November).

Females often showed marked differences in activity at different times of day. Initially, during the greater part of the day, they remained in the tail areas or side of pools, lying directly on the stream bed and showing little if any activity until within approximately 1–2 hours of sunset. Then they moved from the bottom, proceeding to the head of the pool and forming groups. Movement up stream from these pools normally took place at the onset of darkness. Both tagged and untagged fish from the first group released showed this behaviour. The pattern of activity was only disrupted when water levels rose (for example, on 9 November), when fish of both sexes moved actively up stream during daylight.

Progression up stream by the males appeared to be associated with the pursuit of single females and groups of females. The male fish tended to move during the hours of darkness from a down-stream position to join females which had moved up stream in the late afternoon or during the early hours of darkness (for example fish L, Fig. 9).

Females moving through areas of comparatively steep gradient (*ca* 3.5 km, 3.9 km, 5.1 km) with shallow "braided" flow patterns (*ca* 5.1 km) did so intermittently, sometimes stopping in the deeper areas, or indeed in mid-riffle (for example, fish A and D during their initial ascent). However, they often actively traversed shallow areas with the greater part of their head and flanks exposed.

Females were particularly susceptible to becoming temporarily trapped in deeper pockets of water, such as scour holes and lee pools with little water through-flow. Having entered such areas, they would commonly move about actively, before subsequently leaving by the route of entry. Generally, males confined their movements to the part of the channel with the highest flow. Instances of what might best be described as active climbing, rather than swimming, were shown by both males and females. By major flexing of the body and tail these fish moved over stones and through shallow areas less than 10 cm deep. Fishes A and D behaved in this manner during their initial phases of ascent.

Overall, there was a conspicuous difference in the activity between male and female fish. Whereas the females tended to choose a spawning site, spawn, and then move down stream afterwards, male fish spent much longer periods on the spawning grounds, rarely staying in one place and usually showing excursions both up and down stream (Figures 9–14).

Courtship and Spawning

Previous descriptions of the spawning behaviour of Atlantic Salmon have been based upon tank-based observations (Belding, 1934; Jones, 1959; Beall and Marty, 1983). The spawning behaviour has been broadly divided into a number of ordered stages, from the point of initial courtship to the final burial of the eggs. A series of spawnings was observed during this study and the full sequence of behaviour recorded on video tape for sub-sequent analysis.

The female salmon selected particular sites within the burn for spawning, characteristically areas of loose gravel where the flow of water was strong. Spawning usually took place at night. The female initially excavated a small depression in the bed of the stream, the start of the redd, by turning over on her side and vigorously flexing the body and caudal fin, thereby actively displacing the finer sand and gravel down stream. Male fish, either singly or in numbers, previously lying down stream of the redd site, moved up stream and gathered by the side of the female, the individual males reacting aggressively to the intrusion of other males into the immediate area. During

the excavation period, the female repeatedly moved into the pit, dipping her body so that her vent was close to the base of the pit. Eventually, the female dipped down into the redd depression, and on holding this position was joined by one of the attendant males. Both fish then quivered alongside one another with their jaws gaping. At this stage the eggs and milt were simultaneously released into the base of the redd. The eggs dropped into the crevices in the substratum, surrounded by a cloud of milt. Subsequently the female proceeded to an area of undisturbed gravel up stream of the pit, turned opon her side and, flexing her body and caudal fin, displaced sediment which was then washed down stream onto the eggs, burying them. Having completed spawning the female commonly moved down stream away from the redd. Attendant males often remained in the area of the redd and attempted to court other females in the vicinity.

Interactions Between Males and Females

Periods of interaction between males and females were typically brief. Males tended to congregate within or below any length of stream containing females. In the later stages of redd construction by the female, the males moved close, within several metres, repeatedly approaching and quivering. However, clear instances of prolonged courtship of the female were observed only in the later stages of redd excavation. Even where large numbers of males were present, females would often initiate excavation without any observed prior courtship by a male or indeed without any significant periods of close association with the males in the immediate area.

Where isolated pairing of a single male and female occurred, generally away from the main spawning areas, the arrival of an intruding male from down stream usually resulted in the attendant male moving immediately to intercept the intruder. Where an excavating female was in the presence of several males, prolonged courtship was confined to whichever male moved to the side of the female immediately before the final spawning act. Where males fought each other with associated physical contact or repeated interception in the immediate area of an excavating female, it was common for the female to leave the area for short periods, moving either down stream or to one side of the redd site. The males then either displaced one another away from the redd area, or actively followed the female. In general, however, paired males did not follow the female away from the redd. Only where females were in the very early stages of cutting, or in the final stages of redd excavation, characterised by the female showing concentrated cutting and a high frequency of dipping, did the paired male follow the displaced female more than a few metres up or down stream from the redd site. It was more common for the paired male to defend the area of the temporarily abandoned redd pit against intruding adult males, trout and salmon parr.

Incursions into the vicinity of the redd by both trout and salmon parr were particularly evident in the area of the top ford and the south burn confluence spawning grounds (6.44–6.5 km, Fig. 2), especially in the early part of the initial spawning period (10–12 November). Many interactions between the larger male salmon and these intruders were observed, involving lunging movements by the paired male, accompanied by repeated extended jaw movements and rapid turning. This behaviour was shown both in the presence and in the absence of the female. Females behaved similarly on occasions, though with less exaggerated jaw movements, and less frequently than the males, with a shorter path length of pursuit away from the immediate redd site (*ca* 5–40 cm).

At the height of any incursion by intruders (10–12 November), males already paired with a female often devoted most of their time to these activities, at times even displacing the female from the redd area. Repeated contact by the male, including passage over the female's back, forcing the female down into the redd pit, could result in the female moving a short distance up or down stream, away from the site.

Interactions Between Females

In the Girnock burn, with comparatively few spawning females, female interaction was observed on only one occasion (15.15 on 11 November). Physical contact was restricted to flank to flank contact and some displacement. At no time was head-on orientated aggression observed or indeed the erection of the dorsal fin. During the period of observation male fish were not involved. Both fish subsequently spawned within the following 24 hours, having arrived in the area on 11 November.

Interactions Between Males

Interactions between males were evident throughout the spawning season. In some cases, females were present, but it was also noted that there was an increase in aggressive activity between males during the later period of the study, when the sex ratio increased in favour of males as spent females emigrated from the spawning areas.

A range of patterns of male activity is shown in Figures 9–14. Several radio-tagged males moved from the release area to particular short lengths of the burn, eventually spawning there. Male L (Fig 9) is typical. Other males showed more extensive movements between the main spawning areas though still pairing and spawning with females (eg Fish C, Figs. 12 and 14). Further males, particularly grilse, none of which was radio-tagged, showed frequent and extensive movements between the main spawning areas, with few observed successful pairings. These fish attempted pairings with both maiden females and kelts.

Protracted instances of movement up stream from the main spawning areas were observed in several males. These movements commonly coincided with spawning activities further up stream or the movement of unspawned female stock past the male concerned. Itinerant males moving between spawning areas would commonly arrive in the vicinity of a paired cutting female only to be displaced by an attendant male.

Figure 15 suggests that when water temperatures in the burn were low, with ice fringing the stones, for example during the period 19–20 November, and especially when extensive ice cover was evident, for example on 21 November, the excursions made by tagged males were significantly reduced. The most active males moved to and remained within the deeper pools during periods of ice cover. Neither males nor females actively held position in the areas of fastest flow during these conditions.

Male grilse showed very similar movements to multi-sea-winter males, but without exception were displaced by larger males when they met.

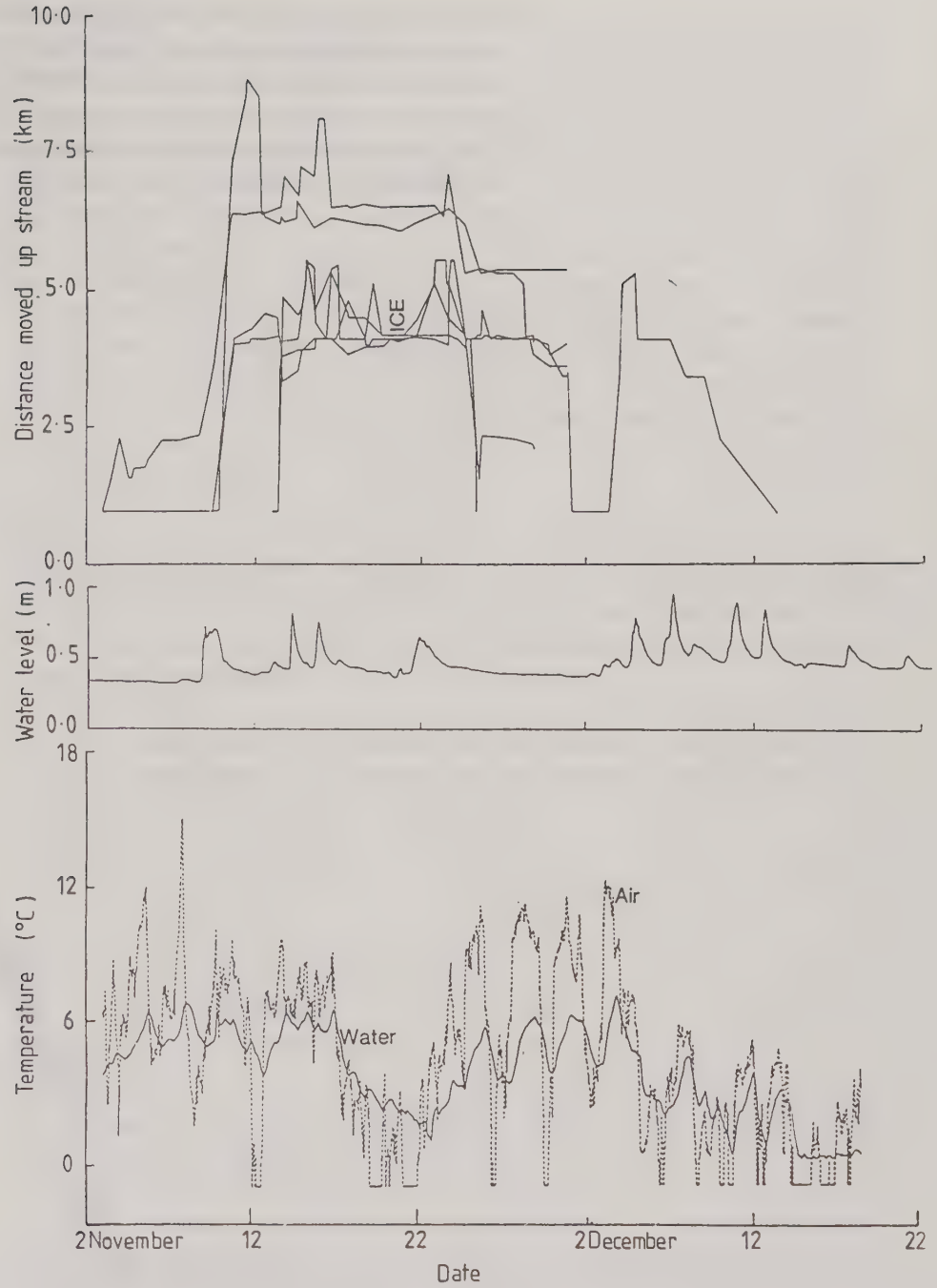

Figure 15. The movements of all the radio-tagged male fish (B, C, E, L, M and P). Note that the activities are concentrated at particular levels within the burn at about 3.5—5.5 km and 6—8 km. The water levels at the Littlemill gauge and air and water temperatures at the trap site are shown.

Redd Excavation

Redd excavation was first observed in the burn at 14.25 on 5 November, with further instances of cutting being observed on 8 and 9 November. The activity was initially restricted to areas of high water velocity, not necessarily those historically associated with spawning activity. Typically they were areas where the flow of water was constricted by the channel topography.

These first excavations proved to be exploratory. The activities of the fish did not appear to result in the deposition of eggs. The females simply produced a limited (a few centimetres) excavation below the normal stream bed level. There was no evidence of any attempt at burial, or of activity being resumed at these sites later in the spawning period.

The first major period of redd cutting activitiy within the main spawning areas was observed on the morning of 11 November and again on the afternoon of 13 November. The last observed incidence was on 4 December, approximately 5.4 m up stream, below the Hampshires bridge (Fig. 2). The final distribution of completed spawning redds of both tagged and untagged fish is shown in Figure 16.

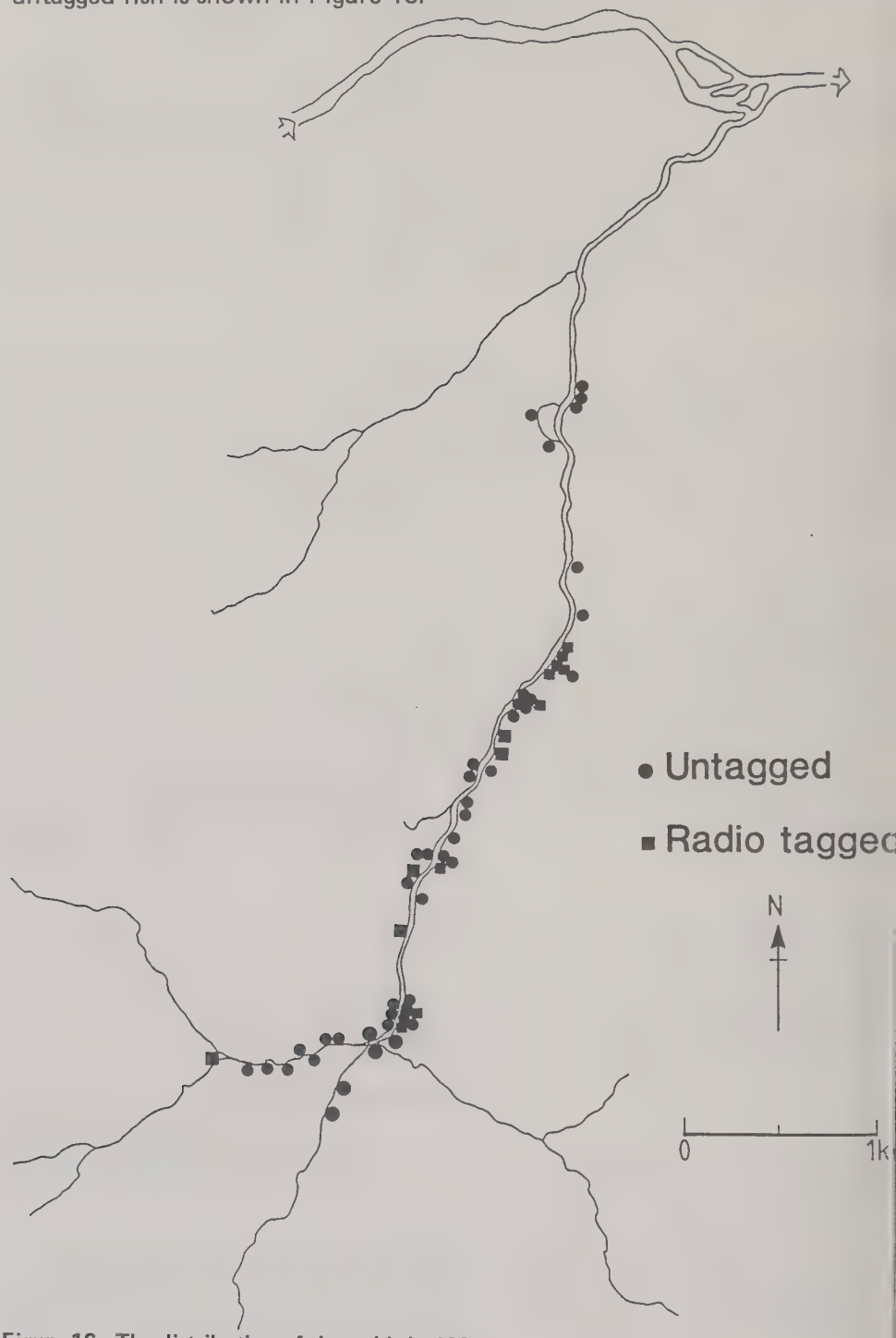

Figure 16. The distribution of the redds in 1986.

Redd excavation was observed both during the day and at night, particularly under moonlit conditions. Those periods when the greatest numbers of females were actively cutting tended to occur after significant increases in stream discharge (Figs. 4, 5, 6, 7 and 8). Females were repeatedly observed approaching potentially suitable areas as water levels began to decline. In the early stages of a decline in discharge, females, whether attended by males or not, shows repeated excursions from holding areas to the potential

spawning areas, often a distance of only a few metres. The period spent in these spawning areas increased as discharge levels declined further. At some point the female would begin to excavate, at first over a wide area, both across and up stream, or with a switch to a new area. As cutting progressed the range of movement declined until activity was concentrated within a comparatively small area, normally less than 0.5–0.3m^2. On a number of occasions apparently unpaired females showed preliminary cutting in the absence of mature male, although the extent of contact with other males and females prior to cutting cannot be accurately assessed. The duration of redd excavation from the initial movements to the final stage spawning ranged from approximately 0.7 hours to over 2 days (excluding prior courtship activities). Extended periods of redd cutting were particularly evident in those fish that spawned after 23 November, both single and multiple spawners. In these fish spawning activities were often confined to the early afternoon.

Table IX illustrates instances of multiple spawning behaviour shown by radio-tagged females. Repeat spawning was observed after varying lengths of time and at different distances both up and down stream of first spawn-of each fish. No female from the second group of tagged fish was observed to cut two or more redds.

Table IX Approximate time separation and net distances moved between separate spawnings for repeat spawning radio-tagged female salmon in the Girnock burn

Fish	Date and time of first spawning	Distance moved between spawning (m)	Time separation
G	11.11 12.00	−107	23h 53 min
J	11.11 13.05	+ 70	7 days
K	11.11 12.40	+628	3 days 13 h
H	12.11 10.12	+189	57 min

Overcutting

Overcutting, the cutting of a redd at a site where spawning had previously taken place, was observed on two occasions.

The first instance took place on 15 November, 4.1 km up stream. Overcutting took place at a redd site established on 11 November by a radio-tagged fish (Fish A, 12 November). The overcutting was performed by a large untagged 2-S-W female, which started cutting at 11.41 and continued until the end of observation at 12.45. Two other females were present in the immediate area, one of which was in the later stages of redd excavation on the same bend. Three males were also present.

The second instance took place on 24 November, the redd being observed in the final stages of burial. The overcutting took place at a redd previously constructed by Fish F on 12 November. An untagged female was observed cutting at this same site at 12.07 on the 24 November.

Post-Spawning Activities of the Female Fish

Having excavated a redd, spawned, and completed the burial of eggs, females sometimes remained on the redd for several hours, lying on the gravel with limited fin movements. More commonly, the fish turned and moved down stream by a combination of both active swimming and passive displacement, with sufficient movement of the body to keep the fish in the main current.

The movements down stream tended to be continuous, interrupted only when the female was intercepted by one or more males or passed through areas of deeper water (0.3–0.5 m). Having reached one of the few large pools, females would typically reorientate themselves to face up stream, and then proceed to an area with some degree of bank cover.

Activity by both day and night, over a range of flow regimes, was then significantly reduced (Figs. 4, 5 and 6) up to the point of initiation of the final down-stream descent. Both fully and partially spent females entered the deeper pools after spawning. Consequently, single females or small groups of two to seven fish accumulated in those pools immediately below the more popular spawning areas, the fish lying together. Males were sometimes present in the same pool, either positioned at the tail, typically a few metres down stream, or in those observed radio-tagged multiple-spawners positioned just to the rear of particular females. Periods of residence by female fish in these holding pools was highly variable, as was the period between the last spawning act and the final descent down stream past the point of release (Figs. 4, 5, 6, 7 and 8).

Females moving down stream from the spawning areas were subject to the repeated attentions of males, particularly when the number of potential spawning females was reduced and water levels were low. Under these conditions male fish were concentrated in pockets of deeper water at the immediate tail of the main spawning areas, particularly in the area of the top ford (Fig. 2). Attempted courtship was evident both immediately after the females arrived in such an area and sometimes when males moved up stream to intercept descending females.

Figure 17 shows the timing of the descent and consequent arrival of spent tagged females at the release point, in relation to the similar movements of untagged females released at the same time. The tagged females descended from the spawning areas rather sooner than the majority of the untagged females. The final down-stream movements of most of the radio-tagged females took place at times of elevated discharge.

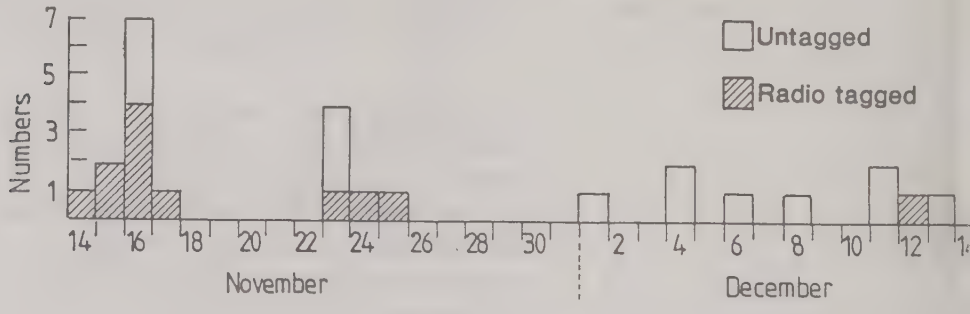

Figure 17. Timing of the return of tagged and untagged females to the release point.

Post-Spawning Activities of the Male Fish

Those male fish remaining within the spawning reaches in the later stages of the spawning period showed a marked reduction in activity. They made fewer of the general excursions described earlier and the frequency of attempted courtship and spawning declined as the number of potential female spawners fell within the middle and upper reaches of the catchment.

Over this period, instances of sporadic fighting and aggressive display became more common, especially in the complete absence of females. During periods of activity, competition for positions at the head of the holding pools and in riffles with the greates flow was evident, with subordinates being displaced to either the marginal or lower reaches of a holding pool.

At this later stage, a considerable proportion of the male population were infected by the common aquatic fungus, *Saprolegnia* sp. As the infections developed, so general activity declined, affected fish spending increasingly longer periods in thos areas of the channel with the least water flow, ie the margins of the larger pools and runs and on the streambed. Some females showed limited infection, with abrasions to the snout and tail-fin edges.

All those larger males (>70 cm) inspected upon descent to the release point showed a range of lesion development on the snout, chin, flanks and fin bases. The rate of physical deterioration in the smaller male grilse was less pronounced than in the majority of M-S-W males.

The Survival of Fish

In general, tagged females spent considerably less time in the burn than the tagged males, fish R and J being the exceptions. Ten out of the 12 tagged females had returned back down stream within 14 days. With the exception of female R, found in an incapacitated state, and female J, removed by an otter, all tagged females of both groups released returned to the descending trap alive and were subsequently allowed to proceed back to the main river Dee. However, of the first group of four tagged males to be released, only one male, fish B, returned to the release point alive. Fish L and E were found dead within the burn (Figs. 9 and 11). Fish C was found dead at the release site. Both tagged males of the second release, M and P, were observed in an incapacitated state below those areas associated with their last observed spawning activities. Of the untagged fish released over the same period, more females survived than males, including both grilse and M-S-W fish.

Discussion

ntry into the Spawning Burn

In the Aberdeenshire Dee, some salmon spawn in the main stem of the river while others spawn in the smaller tributaries. In this study we have examined the movements and spawning behaviour of fish in a shallow tributary prone to wide variations in water flow.

Typically, entry of salmon into very shallow areas, or past obstructions, requires an elevated water level. The water flow requirements for the migrations of salmon have been described by Baxter (1961) and Stewart (1968). The influence of river flow and other factors has also been extensively reviewed by Banks (1969). The magnitude of the fresh-water flow required to influence movement depends upon its duration, the species of fish, river size and time of year (Millichamp, 1976; Stewart, 1969; Peters, Farmer and Radford, 1973).

In the Girnock Burn it seems that there is a primary requirement for the water discharge to be elevated above basal levels before fish will penetrate the catchment. The burn does not appear to provide suitable conditions for the residence of adult salmon over an extended period and entry to the burn is sometimes delayed until late October or early November. From years when extensive Carlin tagging of smolts took place, it is clear that many of the adult fish entering the Girnock were originally spawned there (D.W. Hay, personal communication). These same tagging experiments showed that the returning multi-sea-winter adults may arrive at the Scottish coast and enter the estuary of the Dee as early as February and March, and may subsequently be found within the main River Dee throughout the spring, summer and autumn. Radio-tracking experiments on adult fish returning early in the year to the River Dee have shown that such fish may spend very long periods, several months at a time, at holding positions within the main stem of the river (Hawkins and Smith, 1986).

Though the bulk of adult fish rarely enter the Girnock until late autumn, it is clear from Table X that there is some variation in the timing of entry from year to year, perhaps depending on the flow conditions. Munro (1976) illustrated the relationship between the movements of ascending adults and the discharge of the Girnock Burn over the period 1969–1975 and described the particular events of 1969, when a long period of low discharge (<0.1 m^3 s^{-1}) during the second half of October was followed by a run of 49 fish on 4 November, coinciding with a marked increase in discharge. In some exceptional years, however, small numbers of fish have entered the burn as early as July and August, usually under transient conditions of high flow (Table X).

Table X Time of first capture of salmon in the ascending trap

Year	Date of first capture	No. of salmon entering over year	Date by which 25% the fish had entered	Range of MDF over which fish entered* (m^3 s^{-1})
1966	1.10.66	278	18.10.66	
1967	26.09.67	217	14.10.67	
1968	27.09.68	199	28.09.68	
1969	2.11.69	52	2.11.69	0.48
1970	21.08.70	93	23.10.70	0.25–0.53
1971	18.10.71	133	3.11.71	0.13–0.45
1972	30.10.72	141	30.10.72	0.13–0.79
1973	21.10.73	232	13.11.73	0.30–1.37
1974	8.10.74	190	16.10.74	0.36–1.47
1975	28.09.75	125	4.11.75	0.19–0.94
1976	26.09.76	170	1.10.76	0.59–2.73
1977	7.10.77	119	30.10.77	0.79–2.28
1978	30.09.78	39	3.11.78	0.19–0.69
1979	5.10.79	82	26.10.79	0.59–2.17
1980	17.09.80	199	23.10.80	0.32–1.19
1981	21.09.81	32	21.09.81	1.45–1.83
1982	22.10.82	72	22.10.82	0.44–1.58
1983	17.10.83	65	7.11.83	0.12–0.45
1984	19.10.84	109	26.10.84	0.80–7.79
1985	19.08.85	76	2.11.86	0.76–3.52
1986	30.10.86	161	2.11.86	0.76–3.52

*denotes mean daily flow over which five or more salmon entered the trap.

We observed a strong coincidence between the entry of adults and elevation of burn discharge (Fig. 3), indicating that burn entry is highly dependent upon water flow within the burn. The data in Table X do not, however, indicate that there has been an annually consistent threshold level of flow triggering entry into the burn. The timing of entry in a particular autumn may depend on the pattern of flow during the preceding summer, and the degree of acclimation of the fish to earlier rates of discharge. Thus the increase in discharge required to initiate movement into the burn may be smaller after prolonged periods of low flow in the main river than after a similar period of comparatively high flows, as proposed by Peters *et al.* (1973). Such an effect may either be reduced or exaggerated by changes in the migratory state of the fish. Munro (1976) reported that in the period 1966–1975, 95% of the incidence of burn entry was in October and November, despite the fact that in most of these years quite significant floods occurred in September. Notwithstanding the fact that fish do not invariably enter when flow increases, it does appear that a minimum level of flow is necessary to stimulate entry. Munro (1976) reported that except

on one occasion (7 November 1972) no fish was observed to attempt entry to the ascending trap at discharge levels of less than 0.1 $m^3 s^{-1}$, but on 74 occasions between 1969 and 1975 they entered at flows greater than this. He concluded that mean daily flows of less than 0.1 $m^3 s^{-1}$ limited the entry of fish into the burn, although this conclusion might reflect the tendency to enter the trap within the burn, rather than enter the burn from the main-stem Dee.

It seems likely that there are a great many factors affecting the timing of burn entry, ranging from proximate physical factors such as water flow in the burn, flow conditions in the main river, and the availability of fish in the vicinity of the burn entrance to factors within the fish themselves, resulting from long-term selective pressures.

Having entered the trap and having been tagged and released, some fish proceeded almost immediately to penetrate to the middle reaches of the catchment, moving at flows significantly below those associated with initial entry. The majority, however, waited until flows were once again elevated before moving up stream.

Mills (1968) reported an increased frequency of up stream movement by displaced salmon as the season progressed. After a prolonged period of low flows, movement may take place at flows that under other circumstances would not have provoked movement. Both Hellawell (1976) and Peters *et al.* (1973) suggest the time of year as a potentially important factor in controlling migratory behaviour.

It is possible that in the event of entrance to the burn being delayed, as in 1985 (Table X), some females may spawn elsewhere, either in the immediate vicinity of the burn, at the main river confluence, or indeed in the lower reaches of the burn between the trap and the main river. Spawning activity was observed in the main river before the first major entrance of fish to the trap both in 1986 (personal observation), and in the autumn of 1984 (D.W. Hay, personal communication). Historically, the later the first appearance of adults in the ascending trap the lower the total number of potential spawners that year, although the correlation is poor (A. Youngson, personal communication).

Spawning Behaviour

In general the spawning behaviour described in this study confirms the observations of Belding (1934), Menzies (1931), Jones (1959) and Beall and Marty (1983). Belding (1934) remarked upon the particular "protective awareness" of the female whilst cutting and pointed out that when disturbed she would often leave the redd site but return to the same area later, continuing excavation and associated spawning activities. Male fish were said to return more frequently and on the whole sooner than the female after disturbance. Similar observations were made during the present study.

The popular belief that salmon pair before the initiation of cutting activity, and indeed remain monogamous over the spawning period, was not substantiated. Belding (1934) noted the "insecure" situation that a paired male can be in, as he may be substituted at any time by direct displacement, or indeed over an extended spawning period, by the continual interference of "satellite males". Some males within the Girnock Burn showed intense periods of activity, moving from one female to one or more others. These movements are shown clearly in Figures 9, 10, 11, 12, 13 and 14.

It was apparent over the greater part of the spawning season that some males showed a relatively high frequency of successful sexual activity, whereas others, although very active, showed little evidence of spawning success.

Over the 1986 spawning season there were major changes in the numbers of both sexes at any one location in the burn, particularly in the later stages of the spawning season. The effective sex ratio, ie the number of competent males compared with the number of potential spawning females, changed as the spawning season progressed in favour of males (Table XI), an observation also reported by Menzies (1931).

Table XI The number of salmon captured in the ascending trap 1966–1975 and 1986, and subsequent numbers of completed spawning redds

Year	No. of salmon trapped		No. of females spawned	No. of redds	Spawned female: redd no. ratio
	Males	Females			
1966	113	156	127	124	1:1.0
1967	99	115	106	101	1:1.0
1968	85	111	106	104	1:1.0
1969	19	31	28	25	1:1.1
1970	56	34	29	29	1:1
1971	64	61	61	61	1:1
1972	58	79	70	80	0.9:1
1973	98	127	124	129	0.96:1
1974	79	105	104	103	1:1.0
1975	56	65	60	60	1:1
No redd counts were taken in the years 1976–85 inclusive.					
1986	83(31)**	76(42)**	41	59	1:1.3

*Difference due to females leaving the burn without spawning and loss of potential spawners due to predation

** Number of fish released above trap.

Combined with the males' movements between females, this progressive increase in the ratio of males to females made it very unlikely that females in spawning condition failed to encounter sexually active males.

From these observations it seems that the initial sex ratio (Table III) may be important only under unusual environmental conditions, where there is isolation of a particular part of the burn owing to a barrier restricting the free movement of fish within the system. Normally, over the length of the spawning season there is a reservoir of subordinate males distributed throughout the spawning areas.

Hawkins and Smith (1986) observed comparatively large movements of a radio-tagged male grilse in the main stem of the river Dee. Without the benefit of direct visual observations on the fish they postulated that the male was actively commuting between different areas of the main river, the behaviour being associated with spawning activity.

The amplitude of the movement observed by Hawkins and Smith was typically 3–8 km, rather greater than that observed from males in the Girnock. This might be the consequence of the main Dee being a relatively open and unobstructed system compared with the Girnock. There may be greater ease of movement between different parts of the main river. The distribution of spawning females and of suitable spawning sites may also differ.

From the observations made in this study, the frequency and amplitude of the movements observed was not necessarily an indication that the male had engaged in a number of successful pairings. Indeed, extensive movements may be an indication of a lack of spawning success. A long duration of residence in a comparatively short length of the river may be more indicative of successful spawning.

Movements by a male between females may be potentially profitable in some circumstances. Where spawning is distributed over a number of isolated areas of gravel, with comparatively few females in any one area the behaviour may improve the reproductive fitness of males by producing a greater number of encounters with females. The behaviour may also be advantageous in the later stages of a spawning season when a few scattered unspawned females remain, and the male:female ratio is locally low.

The observations in this study support the conclusions of Hawkins and Smith (1986), that males move more extensively and frequently than females. There appears to be strong commitment on the part of the male to sexually orientated activities over the spawning period, until the physical state of the fish deteriorates, activity is progressively reduced and the fish eventually dies.

Males were evidently able to perceive the presence of one or more females at some considerable distance up stream, over a range of discharges and periods of the day. Belding (1934) described this "attraction at the crucial moment" as occurring invariably before the spawning act. It results in males immediately down stream of the female moving rapidly up stream with no apparent visual or audible signal on the female's part.

This behaviour was observed both during periods coinciding with the initial and final stages of redd construction and also even before a serious attempt at cutting was made by females. Individual females were joined by males over varying distances, often from considerable distances down stream, thereby precluding dependence on auditory or visual cues. An example of this is provided by male Fish C (Fig. 12), which on 3 December between 08.55 and 13.50 moved upstream to join a female. The nature of the attractant in these circumstances is not known, but it may be olfactory. Newcombe and Hartman (1973) observed that rainbow trout (*Salmo gairdneri* Richardson) were strongly attracted to water taken from fish that were actively spawning, but only weakly attracted to the holding water of ripe fish not spawning, under circumstances where both auditory and visual stimuli were ruled out. They went on to speculate that in rainbow trout the role of such chemical stimuli may be important in bringing scattered males and females together in a spawning stream, particularly during periods of nocturnal spawning activity.

Overcutting

On a number of occasions, redd cutting was observed within 0.3 m of an earlier redd site (particularly in the lowest major spawning area (Figures 2 and 16). Hay (1984) stated that during the period 1966 to 1976, even with an adult spawning stock variation of almost five-fold, superimposition of one redd upon another was not observed within the Girnock burn. Table XI shows the spawning populations and corresponding redd totals over this period.

The observation of overcutting during 1986 may have been the result of biological and physical factors. Both spawning areas where overcutting was observed tended to retain their characteristics, in terms of those hydrological factors considered essential for the successful spawning of salmonids described by Baxter (1961), over a wide range of discharge levels. Within other, less favourable areas quite small changes in discharge can result in major changes in the accessibility of spawning gravel. Historically, the two main areas of the Girnock burn where overcutting took place have been associated with the spawning activities of salmon since records began (R.J.G. Buck and D.W. Hay, personal communication).

Carling (1979) described the consequences of artificially regulated discharges at a wide range of levels on a number of existing spawning riffles in the river North Tyne. These studies enabled him to recommend appropriate discharge values both to maintain existing levels of spawning and to enhance those levels. Rantz (1964) described the optimum discharge for the spawning of king salmon, relating characteristics of stream discharge to an index of stream geometry. Further quantitative observations of the spawning activities in relation to the prevailing discharge and stock levels would be required before similar recommendations could be made for the Girnock. It seems likely that each catchment will tend to have its own particular range of optimum discharge, and that within every catchment there will be conservative areas which retain suitable spawning characteristics over a range of discharges and other areas where spawning may be possible only under rather specific flow conditions.

The occurrence and biological consequences of redd-superimposition have long been a matter of some debate. The levels of overcutting observed in the Girnock in 1986 (3% of total redds) would not represent a significant contribution to the total estimated egg mortality (about 6%, according to D.W. Hay, personal communication). Other losses, from such factors as asphyxia, freezing, compaction, predation and displacement are likely to be cumulatively more significant.

Jones (1959) stated that overcutting tended to be a consequence of too many fish on the spawning beds. The numbers of fish entering the Girnock in 1986 were not especially high in relation to those entering in previous years. However, in tributaries of the Hampshire Frome and Piddle, it was concluded (Anon, 1980) that there were usually fewer redds than females, significant proportion of the redd sites (22%) being utilised by two or more females, with time intervals of 1–6 weeks between consecutive excavations. Baxter (1961) concluded that overcutting is most likely at low water levels where there are reductions in the area of suitable spawning gravel. Future studies on the role of discharge regimes in regulating the area of gravel suitable for spawning activity within the Girnock catchment will be needed fully to account for the observations made.

Where it was observed within the Girnock, overcutting was not the consequence of a female moving immediately onto an established redd. It occurred only after appreciable delays, in which major changes in stream discharge occurred. There may have been some changes in the local stream bed topography, especially in those areas subject to the earlier activities of spawning salmon.

Choice of Spawning Site

The choice of spawning site within the Girnock burn appeared to be determined by the female fish. However, there was little evidence of the female fish moving about widely in search of sites. Though some females showed exploratory digging in the lower reaches of the stream they later moved further upstream and settled on their final sites without extensive searching. The range of penetration and final spawning positions within the burn bore little relation to the timing of ascent from the release area. There was some coincidence of spawning time between individuals and the temporary elevation of local discharge levels.

The radio-tagged female fish spawned at different distances up stream and in different locations, making it difficult to examine in detail the relationship between discharge and spawning activity. The observed coincidence of spawning activities by males L and C (Figs. 9 and 12) in a particular area suggests that a significant proportion of the spawning activity took place at particular, elevated discharge levels. However, the discharge levels over which

spawning acitivities took place within different areas of the Girnock burn catchment were different, even within quite short lengths of the burn. Whether the flows required for optimal spawning activity increase as fish penetrate higher into the catchment is unclear.

Figures 4–15 show that the ascent of many adults within the burn, up stream from the release point, depended on increases in burn discharge above basal levels. If we consider that there may be a limited time span within which the female has scope for delaying spawning, then it is apparent that under some flow conditions there may be limited opportunities for female fish to distribute themselves over the full length of the burn. In the event of entry of fish to the Girnock or any other similar catchment being delayed, perhaps through the timing of entrance, which might depend on a single flood, then ascent to the spawning grounds and subsequent spawning may need to take place very quickly, possibly at the first suitable site reached by the fish rather than throughout the burn. Spawning activities may then become compressed into particular parts of the burn, with adverse consequences both for the success of spawning and for subsequent survival of the offspring.

The Tagging Procedure

Figure 17 suggests that the behaviour of the radio-tagged females after spawning may have been different from that of untagged fish. It appears that spent females which were radio-tagged descended from the burn earlier after spawning than those members of the untagged female population.

The effects of transmitter attachment and insertion on fish behaviour are inadequately known (Stasko and Pincock, 1977). McCleave and Stred (1975) recommended internal transmitters for studying the behaviour of hatchery reared Atlantic salmon smolts, and indeed advised against the use of externally placed transmitters. Clearly despite the advantages of the use of radio-telemetry for the study of this kind, the transmitters may cause abnormal behaviour. In the Girnock study, if the procedure, or the presence of the tag in the fish's stomach had modified the behaviour of the fish to any great extent, one might have expected the tagged fish to have shown a difference in general spawning behaviour. One would have anticipated such abnormalities manifesting themselves immediately after release, for example, by a complete failure to spawn, or a failure to migrate up stream upon release, or indeed an attempt to move down stream rather than continuing up stream. Overall, however, the tagged fish did not show a disproportionate tendency to spawn in the lower areas of the burn. They moved to those areas historically known to be suitable for spawning activities. The tagged fish were comparatively well distributed along the length of the burn (Fig. 16) and did not show any marked differences in their spawning behaviour to untagged individuals. The differences shown in the time of down-stream return may simply represent an inadvertent selection of particularly strong and active females at the time of tagging.

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Summary

The movements and spawning behaviour of Atlantic salmon were observed in the Girnock Burn, a small tributary of the river Dee, in the autumn of 1986.

A trap close to the mouth of the burn intercepted all adult fish ascending the burn. The timing of capture of fish at the trap confirmed that water flow in the burn played an important part in stimulating entry and ascent of the tributary.

Eighteen pre-spawning fish from the trap were radio-tagged, released up stream together with 55 untagged fish, and then tracked over a period of 62 days. The activities of all the tagged fish, both male and female, were recorded up to the end of the spawning period.

Males moved more extensively than females, switching between the main spawning areas within the tributary. Except for the latter part of the spawning period, the activities of the majority of males was determined by the distribution and behaviour of females. Courtship and spawning behaviour was observed and described for both sexes.

The tagged females spawned in locations historically associated with spawning within the burn, with spawning site selection undertaken by the female. Some tagged females were observed to spawn in two different locations. Within each batch of fish released, the distribution of spawning activity appeared to be unrelated to the timing of ascent from the release area. However, fish released later in the spawning period tended to spawn lower in the burn. Overcutting of existing completed redds by different spawning females was observed on two occasions.

Over the spawning period, residence within the burn was typically of longer duration for males than females. After spawning, females descended to the nearest deep pool, remaining there for varying periods of time. Subsequent return to the Dee by the females was invariably associated with an increase in discharge within the tributary. In contrast, most males remained within the system until they became physically incapacitated or died.

The role of discharge in the stimulation of burn entry and ascent is discussed, and the possible effects of water flow on the distribution and timing of spawning activity are considered.

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